LIGHT-USE STRATEGIES AND BIOMASS ACCUMULATION OF WOODY SPECIES IN A SUBTROPICAL FOREST IN SOUTHWEST CHINA

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This thesis is dedicated to my parents for their love, endless support and understanding

谨将此论文献给我最挚爱的母亲和父亲，感谢他们对我毫无保留的爱与奉献，支持与理解

CONTENTS

GENERAL INTRODUCTION

Among the >250 000 species of vascular plants inhabiting terrestrial ecosystems, all use the same resources of light, CO2, water and nutrients. All plants utilize the energy supplied by sunlight through the process of photosynthesis to convert inorganic carbon into carbohydrates that provide the basis of survival, growth and regeneration. They also absorb water, which plays a crucial role in all physiological processes, and they acquire nutrients for growth from the soil. The limited availability of water and nutrients within a community as well as the restricted light availability due to mutual shading among plants have puzzled ecologists for decades with a seemingly simple question: how do species stably coexist?

Trade-offs in plant ecology

***One cannot get both [fish and bear's paw] at the same time.* —** Mencius (372–289 BCE)

A trade-off, a term which usually appears in the fields of economy, involves sacrificing one quality of something in order to gain another quality of something else, e.g. money to buy bread. This concept does not only (or even primarily) apply to decisions involving money. Physicists have the same idea when they talk about the conservation of matter and energy. However, the trade-off involved in plant ecology is a less recognized aspect from common life, although it is one of the central mechanisms promoting the diversified life forms on Earth.

The most straightforward trade-offs in plant ecology are those that are physically, physiologically or developmentally enforced. For example, the trade-off between producing a few large seeds versus producing many small seeds has been confirmed by several field studies (Greene & Johnson, 1994, Henery & Westoby, 2001, Shipley & Dion, 1992). Plants with larger seeds tend to have high rates of seedling survival, whereas plants with small seeds benefit from massive seed production (Baraloto, Forget & Goldberg, 2005a, Jakobsson & Eriksson, 2000, Jurado & Westoby, 1992). Another example is the trade-off between specific leaf area (leaf dry mass/leaf area, SLA) and leaf life span (LL). Species with low SLA have been shown to obtain long average LL in diverse ecosystems

(Reich, Walters & Ellsworth, 1997, Wright, Reich, Westoby *et al.*, 2004). It is thought that the structural reinforcement in the leaves with low SLA (thick leaves) renders leaves more tolerant to physical damage and herbivore damage. Higher SLA reflects greater potential for fast growth, high photosynthetic capacity and thus fast return of investment, whereas species with low SLA and high LL have a longer duration of the revenue stream from the initial investment.

Light heterogeneity and light-use strategy

***Forest is not just Swiss cheese.* —** M. Lieberman (1989)

The demonstration of trade-offs in functional traits and plant fitness in nature indicates that natural selection does not allow a "super hero". Instead, natural selection may favor particular combinations of traits, in which case traits form an ecological strategy. Ever since the 1960ies, attempts have been made to define strategies for plants and a variety of strategy schemes have been proposed (see Westoby, 1998). Among those schemes with more than one dimension, Grime's CSR scheme (Grime, 1979) is well known. It introduced three basic strategies for plants: competitor, stress-tolerator and ruderal. There are also other schemes, e.g. Grubb (1998) pointed out plants coping with shortage of resources display one of the three strategies "low-flexibility", "switching" or "gear down". Both examples provided conceptual frameworks of plant strategies, but the lack of practicability to measurements hindered ecologists from testing these strategy schemes.

As species along each strategy continuum exhibit opposite suites of functional traits, functional traits provide a measurable way to study plant strategies. Ecological strategy is "the manner in which species secure carbon profit during vegetative growth and ensure gene transmission into the future" (Westoby, 2002). Securing carbon profit does not mean that species are selected to achieve maximum short-term carbon gain rates. Competition for resources forces species to vary in growth, defense and storage from opportunistic (usually associated with high growth and low survival) to conservative (low growth, high survival) strategies. The opportunistic strategy, analogous to the r-strategy in life-history theory

(Pianka, 1970), is represented by a suite of functional traits optimized to achieve fast growth over a short term. Conversely, species of the conservative strategy (K-strategy) do not grow fast, but they invest more energy to defend themselves against herbivores and pathogens. Thus, in the long term they can maintain positive carbon balance in low-resource environments (Kitajima, 1994). As a broad generalization, opportunistic and conservative strategies also parallel early- and late-successional (Bazzaz, 1982) or ruderal vs. competitive strategies (Grime 1979).

Among all the resources plants need to grow in tropical and subtropical forest, light is the most limiting resource for seedling performance. There is large light heterogeneity in these ecosystems. For example, the light condition at the bottom of a dark tropical forest is in the order of 0.5–2% of above-canopy light (Chazdon, 1988, Clark, Clark, Rich *et al.*, 1996). Moreover, canopy stereogeometry, seasonality and dynamics of gap formation also account for light heterogeneity experienced by plants. There is wide variation in the light environment encountered by seedlings after emergence. Some emerge into fairly open area (e.g. a newly formed forest gap), while most emerge under forest canopy which intercepts a large proportion of sunlight. The dichotomy of the above-mentioned plant strategies is between a light-demanding (opportunistic) and a shade-tolerant (conservative) strategy. At one end of the strategy spectrum, light-demanding species grow fast where there is high light and tissue loss is not too great and die fast when overtopped by other plants; at the other end, shade-tolerant species grow slowly but persistently even with limited light in forest understory (Denslow 1980, Pearcy and Sims 1994). As a broader generalization, light-demanding and shade-tolerant species exhibit opposite suites of seedling traits and performance which may reflect the ecological niche of the species. The interaction between the interspecific response to light (both traits and performance) and light heterogeneity can promote species coexistence. Such plant strategies are also reflected in patterns of functional trait correlations (Westoby, Falster, Moles *et al.*, 2002).

***Competition in a given environment favours plants whose form and physiology maximize their net rate of carbon gain there.* —** T.J. Givnish (1988)

The fundamental assumption is that tolerant species possess enhanced carbon-capture abilities under conditions of low light. However, in one synthesis of tropical tree seedlings, Veneklaas & Poorter (1998) show that intolerant species can have increased growth potential (e.g. greater leaf area ratios) in both gaps and understory light environment.

Besides trade-offs between functional traits, trade-offs also manifest themselves in terms of whole-plant fitness, that is a higher fitness under one set of conditions may reduce the fitness under another set of conditions (Macarthur & Levins, 1964, Tilman, 1988). Trade-offs reflect specializations in ecological space defined by spatial and temporal heterogeneity, and ultimately constrain the environmental species span. At least two types of fitness trade-off have been suggested. One school of thought believes in trade-offs along gradients of microclimate. Take light conditions in the forest for example. Light-demanding species with high growth rate in forest gaps should grow slowly in the shade, whereas shade-tolerant species, which grow more slowly than light-demanding species in gaps, should grow faster in the forest understory through morphological acclimation to shade, e.g. higher SLA (Givnish, 1988, Thomas & Bazzaz, 1999, Sack & Grubb, 2001, Sack & Grubb, 2003).

Another school of thought suggests species which grow faster in the light also grow faster in the shade, while there is a trade-off between high-light growth rate and low-light survival, i.e. seedlings of light-demanding species have high growth rate but generally low survival, whereas seedlings of shade-tolerant species have low growth rate but high survival (Kitajima, 1994, Pacala, Canham, Saponara *et al.*, 1996, Poorter, 1999). This hypothesis has been supported in various communities (Gilbert, Wright, Muller-Landau *et al.*, 2006, Kitajima, 1994, Reich, Tjoelker, Walters *et al.*, 1998). Such trade-offs arise from the very opportunistic to the very conservative ends of the trade-off continuum. Opportunistic species emphasize growth over defense while conservative species emphasize defense over growth. The opportunistic strategy is represented by a suite of

functional traits optimized to achieve fast relative growth rate (RGR) over the short term. Species may experience large setbacks in biomass.

Traits, plant performance and community assembly

There is growing interest in the possibility that functional traits provide insight into ecological differences among species, species interactions and ecosystem processes (McGill, Enquist, Weiher *et al.*, 2006, Reich, Wright, Cavender-Bares *et al.*, 2003, Wright, Leishman, Read *et al.*, 2006, Clark, Dietze, Chakraborty *et al.*, 2007). Functional traits refer to measurable properties of organisms that strongly influence or are strongly coordinated with ecological performance. Community assembly rules are thought to shape the distribution and the mean value of functional traits through two opposing forces. First, the filtering effect of environmental conditions eliminates those traits which are not suitable for a certain condition. This effect results in the connection between functional traits and environment, which has already been recognized since early times in plant ecology. For example, Schimper (1898) found that different functional types of plants are successful in different environmental conditions. More recently, Diamond (1986) argued for "habitat first" models representing the importance of filtering. Keddy (1992a) defined the filter effect in a broader sense, as filters of any kind that remove species that lack of traits necessary for persistence under a certain environmental condition. A hierarchical set of filters including climatic conditions, disturbance regimes and biotic interactions was found to determine the optimal trait values in a community (Diaz, Cabido & Casanoves, 1998, Keddy, 1992b, Egli & Schmid, 2001). Second, high levels of trait variation due to limiting similarity are also often observed within communities (Ackerly, Knight, Weiss *et al.*, 2002, Cornwell & Ackerly, 2009, Wright *et al.*, 2004). The large variation of traits observed in nature has fascinated ecologist ever since Darwin's time (Chapter II, Darwin, 1859). Trait variation comes from two sources: phenotypic plasticity, which permits a certain genotype to produce a range of trait values as a response to environmental variation, and heritable differences between species resulting from evolution (Keddy, 1992a).

Predicting species distribution and abundance is the main aim in community ecology. Can functional traits be the right tool to help us to gain a better understanding and make better predictions in community dynamics? To answer this question we need to understand the linkage between functional traits and plant performance.

Growth and survival are the two vital phenomena for any living organism (Hunt, 1982). These features in seedlings can largely drive forest composition and dynamics (Clark & Clark, 1992, Kobe & Coates, 1997, Pacala *et al.*, 1996). Previous studies have been exploring the key determinants of growth and survival in herbaceous and woody species, however, there was not a consistent result obtained from these studies (Meziane & Shipley, 1999, Poorter & Remkes, 1990, Poorter & Van der Werf, 1998, Poorter, 1999, Walters, Kruger & Reich, 1993). Differences in growth form of studied plants might have led to the inconsistent results. Yet discrepancy remained among studies confined only to woody species. For adult trees and saplings, Poorter & Bongers (2006) found that leaf traits were closely associated with growth, survival and light requirements of plant species in a semi-evergreen tropical moist forest community, while Wright *et al.* (2010) found wood density alone explained >80% of the total variation in a growth vs. survival trade-off for 103 tree species from Barro Colorado Island, Panama. For woody seedlings, Cornelissen et al. (1998) found leaf morphological traits (leaf area ratio and specific leaf area) to be the most important variables explaining interspecific variation in RGR in 97 European woody species, while Veneklaas & Poorter (1998) and Shipley (2006) conducted meta-analyses and found that a plant physiological variable (net assimilation rate) explained most of the variation in growth rate.

Several reasons can account for the inconsistent results above. First, the main constrains on plant growth and survival may not be the same in shade-house experiments and in the forest understorey. In shade-house experiments, besides the difference in light availability, plants are grown under near-identical conditions and are deprived of competition with other plans or herbivore damage. In contrast, in the forest understorey plants experience multiple stresses exerted by competitors, shortage of nutrient and water, pathogens, etc, so that they may have to invest more energy into defense and storage. Some studies found that demographic rates could be largely affected by the partitioning of

resources between different plant organs and the morphology of organs. Resource allocation theory predicts that plants should allocate more resource to organs that capture the most limiting resources. Thus, proportionally more roots will be produced when there is nutrient deficiency and more leaves when a plant is experiencing deep shade (Reich *et al.*, 1998).

Critical seedling stage

"What a feeble beginning for so long-lived a tree! By the next year it will be a star of greater magnitude, and in a few years, if not disturbed, these seedlings will alter the face of Nature here" — H.D. Thoreau (1993)

Responses of seedlings to extremely low light have received more attention than any other type of stress because responses of seedlings are a key component of successional and gap dynamics in dense forests (Bazzaz 1996). The seedling stage is the critical stage in a plant's life cycle. Studying seedlings of woody plants in their natural habitat is important because of the high mortality often incurred during this stage of the life cycle (Harper, 1977, Silvertown & Charlesworth, 2001). Because of their small size, seedlings are more susceptible to resource limitation. Even a small deduction in biomass can lead to the death of a seedling. So, the losses of seedlings in nature are usually high. Thus, the differences among species with regard to the environmental requirements of seedlings can play an important role for the long-term coexistence of adults.

In an evolutionary context

Only those variations which are in some way profitable will be preserved or naturally selected. — C. Darwin (1859)

The species and functional traits as we can see today have both been selected by evolution. The differences among species that co-occur in an ecological community are the result of modifications to a common ancestor that the species all ultimately share. Darwin has

already stated the similarity of closely related species (same genus); species interact with each other based on phenotypic differences and similarities which was formed through evolution. Furthermore, trait correlations across species can also arise by correlated evolutionary divergence of traits deep in the past in phylogeny, thus within each of the descendant lineages trait combinations persist. It has also been argued that species within local communities tend to be phylogenetically overdispersed (Carvendar-Bares et al. 2004). Thus to identify if an ecological spectrum observed today indicates correlated evolutionary changes in the past or is merely the result of a common ancestor, we need to study it in an evolutionary context (Felsenstein 1985, Webb 2002).

Study area

All field experiments and studies used to produce this thesis were located in Dujiangyan, southwest China. Dujianyan lies in one of the 11 biodiversity hotspots of China. It is the place with strong differentiation of species. Climatically it belongs to the north-subtropical zone, mid-subtropical zone and the Tibetean plateau region, influenced by the southeast monsoon from the Pacific in summer (May–October) and by southern winds from the Tibetan plateau in winter (Novermber–April). Thus, the region has dry, temperate winters and rainy summers. The annual average temperature is 15.2 °C. January average temperature is 6 °C and July average temperature is 25 °C. The mean annual precipitation is 1300–1800 mm and the annual average relative humidity is above 80%. The vegetation is composed of evergreen broad-leaved forests of the mid-subtropical zone, evergreen and deciduous broad-leaved mixed forest of the north-subtropical zone, southern deciduous oak forests of the warm-temperate zone, cold-temperate coniferous forests on mountains and high-cold shrub-meadows. The unique transitional location of Dujiangyan provides the opportunity for a large number of plant species to coexist. The large diversity observed in the forest community in this region provided the basis to study niche differentiation between species with various strategies. The coexistence of both deciduous and evergreen species enabled me to compare coexisting plants with different leaf habits (Chen, 2000).

Thesis outline

The main topic of this thesis is the spectrum of light-use strategies among coexisting species and the corresponding functional trait spectrum. I first study variation of seedling growth rate, survival, functional traits and the linkage between these traits along a light gradient in a shade-house experiment (**Chapters 1 and 2**). Then I pursue how environmental variables as well as seasonality influence performance and functional traits of seedlings in the forest understory (**Chapter 3**). Finally, I look into life-history strategies of adult trees (when light is no longer the major limiting resource), based on the variation of leaf and wood traits, and investigate the level of natural selection on functional traits and their correlations (**Chapter 4**). With Chapter 1 and 2, I gain knowledge of inherent species differences (in growth, survival and functional traits) in response to different light conditions, light being the major varying environmental variable. With Chapter 3, I study the species in the natural forest understory where multiple stresses occur, comparing the plants with seedlings studied in isolation in Chapter 1 and 2. Instead of the species-centered view in previous chapters, Chapter 4 stresses multilevel trait variation and covariation in an evolutionary context, so as to understand niche differentiation between species and the ecological spectrum of functional traits, in order to gain a holistic understanding of coexistence within a community in the light of niches, variation and evolution.

In **Chapter 1**, I examine plant growth rate and functional traits (physiological and morphological traits, biomass partitioning) in seedlings of 14 woody species in a 2-year shade-house experiment. Seedlings were grown under a light gradient of 3%, 17%, 44% and 100% full light. The observed differences reflect habitat niche differentiation between species employing contrasting ecological strategies. Growth rates are estimated based on a mechanistic model which incorporates temperature and light. I then explore which functional trait explains most of the variation in growth rate at a certain light availability in both a time- and a size-standardized manner.

In **Chapter 2**, I examine the survival rate among seedlings of 14 subtropical woody species along a light gradient over two years. Together with the growth rate data obtained from Chapter 1, I investigate the performance trade-off which could potentially contribute to coexistence. Two types of trade-offs are of interest: (1) a trade-off in growth rate between high and low light and (2) a trade-off between growth in high and survival in low light.

In **Chapter 3**, I report results from a transplanting experiment in which I study the mortality and growth of seedlings from 14 subtropical woody species grown along a natural light gradient in the forest understory. I aim to identify how functional traits, functional type, seedling age, seasonality and multiple stresses experienced by plants influence seedling performance in the field.

In **Chapter 4**, I study the leaf-wood economic spectrum in adult trees and shrubs coexisting in subtropical forest. I assessed three leaf traits, leaf half-life (LHL), leaf mass per area (LMA) and nitrogen concentration in green leaves (N_{green}), and a wood trait, wood density (WD), in 295 individuals belonging to 45 tree or shrub species from September 2006 to January 2009. Using multilevel ANOVA and decomposition of sums of products, I estimate the amount of trait variation and covariation among taxa, functional types (deciduous vs. evergreen), growth forms (trees vs. shrubs), individuals and seasons. I also examine the phylogenetic signal in, and, using phylogenetically independent contrasts, the evolutionary coordination of these traits.

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CHAPTER 1

Net assimilation rate determines plant growth: a growth analysis of 14 subtropical woody species across a light-availability gradient

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Abstract

The influences of light, ontogeny and plant size on relationships of relative growth rate (RGR) to physiological and morphological traits were examined for seedlings of 14 subtropical woody species (seven evergreen and seven deciduous) over two years in a shade-house experiment. The traits included the three growth components net assimilation rate (NAR), specific leaf area (SLA) and leaf mass ratio (LMR) as well as other gas-exchange traits. Seedlings were grown under 3%, 17%, 44% and 100% of full daylight. Height and stem diameter were measured every two weeks and plants of each species were harvested one and two years after transplanting. We developed a mechanistic growth model to predict the daily growth of each seedling based on a power-law function together with environmental conditions (temperature and light). With this model we could estimate RGR for each species on any given day. We calculated the contribution of each trait to RGR at each harvest date and at common plant sizes. RGR of each species increased with increasing light (up to ~40% of daylight), and decreased with increasing size. Increasing light was correlated with increasing NAR and decreasing SLA, and had no effect on LMR. NAR made the largest contribution to RGR, regardless of light availability. Nitrgen content and photosynthetic capacity on a mass basis were also positively correlated with RGR under most light conditions. We also found positive interspecific relationship in RGR−SLA and RGR−NAR, and moderately negative relationship in RGR−LMR, all of which were stronger when considered at a common plant size. Our results showed that irrespective of light conditions, physiological traits determined the growth of woody plants while biomass partitioning had little effect.

Introduction

Growth is vital phenomenon for any living organism (Hunt, 1982). Particularly in plants, growth is of paramount importance as both survival and reproduction depend on plant growth. Even under a constant environment, large interspecific variation have been found in the relative growth rate (RGR) of plants (Grime & Hunt, 1975, Garnier, 1992, Poorter & Remkes, 1990). These differences in species-specific RGR are important because they influence community structure and dynamics (Tilman, 1988, Grime, 1979). What factors cause some species to grow faster than others under particular environmental conditions? To obtain more insight into this question, RGR is often factored into net assimilation rate (also called unit leaf rate; NAR, g cm^{-2} day^{-1}), specific leaf area (SLA, cm^2 g^{-1}) and leaf mass ratio (LMR, g g^{-1}) (Hunt, 1982, Evans, 1972) as:

$$RGR = NAR \times SLA \times LMR \qquad \text{(Eq. 1)}$$

NAR is the increase in plant weight per unit leaf area and is a complex physiological variable, usually correlated with photosynthesis and respiration (Konings, 1989, Poorter, 1989). SLA is the leaf area per unit leaf mass, a morphological characteristic of plants. LMR is the ratio between leaf biomass and plant biomass, reflecting the proportion of plant biomass invested into leaves.

Plant ecologists have been studying the inherent variation in plant growth and exploring the determinants of relative growth rate over the last few decades. Studies comprehensively examined growth parameters mainly of herbaceous species (Poorter *et al.*, 1990, Garnier, 1992, Garnier, 1991, Vanderwerf, Vannuenen, Visser *et al.*, 1993, Maranon & Grubb, 1993), a few on woody species (Portsmuth & Niinemets, 2007, Walters, Kruger & Reich, 1993b, Bloor & Grubb, 2003, Poorter, 1999) and occasionally on a combination of both (Meziane & Shipley, 1999). Contrasting results have been reported in these studies. For example, Garnier (1992) found NAR determined RGR while Poorter *et al.* (1990) showed SLA had the best correlation with RGR and Brewster & Barnes (1981) found an overwhelming influence of LMR on RGR. To avoid drawing a general conclusion from a small number of species, a few meta-analyses covering a large number of species have been conducted, e.g. by Poorter & Van der Werf (1998) for herbaceous plants, by

Cornelissen *et al.* (1998) and Veneklaas & Poorter (1998) for woody plants, and by Shipley (2006) for both woody and herbaceous species. Yet discrepancy still remained: Poorter & Van der Werf (1998) and Cornelissen *et al.* (1998) found LAR to be the most important variable in explaining interspecific variation in RGR while Veneklaas & Poorter and Shipley found that NAR explained most of this variation.

There are several possible explanations for the inconsistent patterns observed in the relationship between plant functional traits and RGR. First, the relative influence of functional traits on RGR may vary with environmental factors, in particular irradiance. One hypothesis is that RGR is determined primarily by SLA under low irradiance and by NAR under high irradiance, thus the compensatory influences of SLA and NAR on RGR between low and high light would limit variation in RGR in heterogeneous light environments (Meziane *et al.*, 1999, Shipley, 2002). The relative influence of functional traits on RGR can also vary with age (Villar, Maranon, Quero *et al.*, 2005). Second, plant biomass allocation changes during development as a function of plant age or size (Muller, Schmid & Weiner, 2000). As plants increase in size they become less efficient in terms of biomass accumulation because of increased allocation of biomass to non-assimilating tissue, increased respiration costs, self-shading and other growth constraints. Thus plants usually have decreasing RGR when they grow larger (Evans, 1972, Hunt, 1982, Coleman, McConnaughay & Ackerly, 1994). Furthermore, plant functional traits can also vary with plant age (Walters *et al.*, 1993b, Poorter & Pothmann, 1992). Therefore, meta-analyses including plants of different age, spanning from days to months or years, could bring bias to the results and the size-dependency of plant functional traits and RGR require interspecific comparison to be controlled for plant size (Coleman *et al.*, 1994, Rees, Osborne, Woodward *et al.*, 2010). Third, a particular species or functional types adapted to a specific environment may exert a decisive influence on the relations between RGR and traits. Therefore, investigations with a large number of species which have large differences in inherent RGR and include contrasting functional types are the most appropriate to explore this question.

The above-mentioned concerns in growth analysis showed the great need of a study covering a large number of species varying in inherent growth rate grown under an

irradiance gradient to disentangle the relationship between plant functional traits and plant growth rate. Thus we carried out a two-year growth study on seedlings of 14 woody species grown under four different light levels. We examined the responses to light in the three growth components (SLA, LMR and NAR) as shown in equation 1. Besides, we also examined biomass partitioning to other organs (stems and roots) to understand whole-plant carbon allocation, as well as gas-exchange attributes and nitrogen content of leaves to gain insight into plant physiological variation and chemical status in response to irradiance. In contrast to traditional approaches, we estimated size-standardized RGR (SGR) from a mechanistic model, which allowed us to estimate instantaneous SGR at the day of harvest and to relate it to the functional traits measured on the same day, thus precisely evaluating the relationships.

In this chapter, we first examine species difference in size-standardized relative growth rate in response to a light gradient. We then determine how seedling physiological, morphological, biomass partitioning traits influenced by plant age, light availability, functional type (evergreen versus deciduous) and species identity. In the end we explore how the variation of functional traits influence the variation of species SGR under different light availability, and determine which of the three growth components (NAR, SLA and LMR) makes the most contributions on SGR. As plant biomass may have large influence on plant physiology and growth, we further ask whether the results change if we correct for size-dependency of functional traits and SGR.

Materials and Methods

Study site and species

The experiment was carried out from August 2007 to July 2009 in an experimental garden near Dujiangyan, southwest China (31˚04’ N, 103˚43’ E). The climate in the region is characterized by a mean annual temperature of 15.2°C and an average July temperature of 25°C. The mean annual precipitation at Dujiangyan is 1341 mm with a dry season in winter (November–April) and with warm and rainy summers (May–October). The annual average

relative humidity is above 80%. The vegetation in the region can be classified as a secondary conifer and broad-leaved mixed subtropical forest (Chen, 2000).

The 14 species used in this study are all woody species commonly found in the study region (species information see Table 1). These species were selected according to their leaf habit, successional status and seedling availability. There were seven broadleaved-evergreen and seven broadleaved-deciduous species. The deciduous species are either early-successional (*Alangium chinense, Castanea henryi* and *Rhus punjabensis*) or intermediate. In evergreen species, *Pyracantha fortuneana* and *Lindera communis* are early-successional, *Phoebe zhennan* is late-successional and the rest are intermediate (ECCAS, 1974–1999). In the following, all species will be referred to by their short name only (Table 1).

Experimental design

Fifteen shade houses were arranged in a 3 × 5 grid with a 2 m distance between shade houses. These shade houses represented three light levels with five houses as replicates for each level. The light levels were created by covering shade houses with layers of neutral shade netting with different density. The shade houses had a height of 2.2 m, and an area of 4 × 5 m. Instantaneous PAR (Photosynthetically Active Radiation) readings were made both outside and inside each shade house using an SKP 215 PAR Quantum sensor (Skye Instruments ltd, UK). These measurements indicated that the plants were receiving 43.7±2.1%, 17.1±0.73%, 2.74±0.1% of full daylight in the high-, medium-, and low-light shade houses. The light condition gives a good simulation to the natural light gradient in the forest as 50% is usually encountered in open areas and 3% in understory of subtropical forests in the region (observations by the author). To avoid environmental heterogeneity affecting experiment results, we applied a random-block design, i.e. each of the three light levels occurred once in each block of three houses and was positioned in a random sequence. The fourth light level (full daylight) was performed outside of the shade houses. We marked 5 quadrates next to each other besides the area of the shade houses, with at least a distance of 1 m between quadrates.

Air temperature and soil temperatures were measured with a Hobo U12-015 temperature data logger (Onset Computer Corporation, 470 MacArthur Blvd., Bourne, MA 02532, USA). We hung one thermometer in the air inside one of the shade houses and buried another thermometer 10 cm below the top soil in the same shade house. Measurements were taken every hour from day 58 until the end of the experiment, and mean daily temperatures were calculated.

Growth of the plants

Seeds were collected from under parent trees in subtropical forests in the Dujiangyan region in spring 2007. All seeds were processed on the day of collection. Seeds were then germinated under a shade cloth in a nursery. In August 2007, the seedlings were individually transplanted into plastic plots (30 cm height, 30 cm diameter) filled with farmland top soil. Two seedlings from each of the 14 species were placed into each shade house and in each full-light quadrate, yielding a total of 560 pots with a single test plant each. The pots were arranged in a hexagonal pattern with a distance of 0.5 m between neighboring pots (0.8 m between the centers of neighboring pots) to avoid shading. Two weeks after moving pots to shade houses, we replaced dead seedlings with ones of the same species sown at the same time. Plants were watered every 3–4 days or when the soil was dry.

We measured the stem height and basal diameter on each seedling every two weeks and destructively harvested subsets of seedlings in August 2008 and July 2009, reflecting different ontogenetic stages during plant growth. After the harvest in August 2008, we moved and re-randomized the remaining seedlings between shade houses of the same light level to avoid plant growth responses due to the heterogeneity of light within shade houses. Meanwhile, we observed several seedlings from Ca and Rp growing in high light had reached a height of 1.5 m. To avoid nutrient limitation and mutual shading of pots, we transplanted all seedlings from pots into the ground. The total seedling number at each harvest was 286 (August 2008) and 214 (July 2009).

Measurements on physiological, morphological and biomass partitioning traits

At each harvest, the cumulative leaf area and leaf, stem and root mass were determined. Each seedling was separated into leaf, stem and root fractions. We used a LI-3100C Area Meter (LI-COR company, Lincoln, NE, USA) to determine the total fresh leaf area of each seedling. Afterwards each fraction of seedlings was oven-dried at 60°C for 72 h until a constant mass, and weighed to the nearest mg. Specific leaf area (SLA, $cm^2\ g^{-1}$) was calculated as the ratio between cumulative leaf area and leaf dry mass. Leaf mass ratio (LMR, %), stem mass ratio (SMR, %) and root mass ratio (RMR, %) were calculated as the ratio between biomass of each part to total plant biomass. Net assimilation rate (NAR, mg $cm^{-2}\ day^{-1}$) was calculated by rearranging equation 1 that (RGR was estimated with growth model as explained in following paragraphs)

$$NAR = RGR / (LMR \times SLA) \qquad \text{(Eq. 2).}$$

Leaf thickness (T, mm) was measured with a field caliper at several locations (not on the leaf veins) on two fully expanded leaf blades of each seedling at the final harvest. Total nitrogen content (N_{mass}, % dry mass) of these leaves were determined with a CHN analyzer (Leco CHNS–932, Leco instruments, St. Joseph, MI, USA) in the Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Switzerland. Leaf nitrogen content per area (N_{area}, g m^{-2}) was calculated as $N_{area} = N_{mass} / SLA$.

Gas-exchange measurements

Leaf gas-exchange response to irradiance was measured in mid-height fully expanded leaf of one plant per species and light treatment combination. We used a portable photosynthesis system Licor-6400 (LI-COR Biosciences, Lincoln, USA). The instrument was adjusted to have a constant flow (500 μmol s^{-1}) inside the leaf chamber. The CO_2 concentration in the chamber was the same as that in the environment. Leaf gas-exchange rates were measured at 8 light intensities of PAR obtained by using a red-blue light source sequentially at 1500, 1000, 750, 500, 300, 150 and 0 μmol $m^{-2}\ s^{-1}$ in order to reduce the equilibrium time required for photosynthesis induction and stomatal opening. Each leaf

was kept for maximum 2 min at the same light intensity in the leaf chamber. Rate of photosynthesis (A, μmol CO_2 m^{-2} s^{-1}), stomatal conductance (gs_{area}, μmol H_2O m^{-2} s^{-1}) and Vapor Pressure Deficit (VPD) which was a variable representing the relative humidity and temperature in the chamber were recorded at each light intensity once leaf reached the equilibrium status. A were plotted against incident PAR, and the resulting curve was fitted by the Mitscherlich function $A = A_{max}[1-e^{-A_{qe}(PPF-LCP)}]$, where A_{max} represents the asymptote of photosynthesis at high light, A_{qe} corresponds to the initial slope of the curve at low light levels (known as apparent quantum yield), PPF is photosynthetic photon flux, LCP indicates the x-intercept of the curve (known as photosynthetic light compensation point) and A is net photosynthesis, the response variable (Peek, Russek-Cohen, Wait *et al.*, 2002, Potvin, Lechowicz & Tardif, 1990). Parameters of the model were calculated by function *nls* run from R 2.12.2 (R Development Core Team 2011; http://www.r-project.org). To be in accordance with annotation of other variables, we used A_{area} (μmol CO_2 m^{-2} s^{-1}) instead of A_{max} to indicate the maximum leaf CO_2 assimilation expressed on an area base. We then calculated $A_{mass} = A_{area} \times SLA$, which was the maximum leaf CO_2 assimilation expressed on a base mass (nmol CO_2 g^{-1} s^{-1}). Photosynthetic N-use efficiency (PNUE) was calculated as A_{mass}/N_{mass} (Field & Mooney, 1986).

Due to the varying temperature and humidity of environment, the mean VPD for individuals varied from 0.36 to 3.04. We found photosynthetic rate had significant negative correlation with the value of VPD. To avoid the error on photosynthetic rate introduced by the varying VPD during the measurements, we gradually discarded the gas-exchange data at the both ends of the distribution of VPD until the correlation between VPD and photosynthetic rate was not significant ($P>0.01$). Thus the data used in this study covered a range of VPD from 0.85 to 1.95, 18 to 88% quartile of the original VPD distribution.

Biomass estimation

We used data from the destructive harvests to estimate biomass at each non-destructive harvest. We regressed stem volume (StemV in cm^3) against biomass (M in g dry mass) to estimate seedling biomass (Kohyama & Hotta, 1990). In our study, StemV was highly

predictive of biomass (R^2 = 0.76). As species identity, light treatment and their combinations may influence allometry, species-, light-, and species×light-specific regressions were calculated. When we compared observed and estimated M from the different methods we found that light-specific regressions gave the best estimates (highest correlation coefficient estimated M ~ observed M, R^2=0.79). Thus we used the predicted biomass from these regressions in our growth model. For the 3% light treatment we used ln(M) = 0.065 + 0.88 ln(StemV); for the 17% light treatment ln(M) = 0.448 + 0.909 ln(StemV); for the 44% light treatment ln(M) = 0.671 + 0.953 ln(StemV); for the full light treatment, ln(M) = 0.757 + 1.033 ln(StemV).

Plant growth modeling

Plants often have irregular growth rates, reflecting the vagaries of environmental conditions such as temperature and light. Such temporally-varying predictors are not easily incorporated into classical analyses of plant growth, rooted as they are in the statistics of ordinary least squares. To allow for such variations, we used a mechanistic growth model that predicted the daily growth of each plant given its current size, light availability, and the environmental conditions on that day (Turnbull, Paul-Victor, Schmid *et al.*, 2008). Since plants become increasingly inefficient in terms of biomass growth when they grow larger, we developed our growth model based on a power-law function (Paine *et al.*, 2011). The daily environmental conditions temperature and light were incorporated in the following way. For a given plant *i* and day *d* (days after the start of the experiment), the daily growth model calculated daily biomass gain as:

$$C_{i,d} = T_{i,d} \times L_{i,d} \times G0_i \times M_{i,d}^{\beta_i} \qquad \text{(Eq. 3)}$$

Here G0 is a growth constant, M is the whole-plant biomass and β governs the rate of slowing as biomass increases. $T_{i,d}$ adjusts growth according to daily temperature and $L_{i,d}$ adjusts growth according to light availability.

Daily biomass gain is taken as a three-parameter logistic function of temperature:

$$T_d = 1 + \frac{T_{cp} - 1}{1 + \exp[(T_{obs} - T_{mid})/T_{sc}]} \qquad \text{(Eq. 4)}$$

As the observed temperature T_{obs} increases, T_d approaches 1, thus temperature does not reduce biomass gain. Contrastingly, as T_{obs} decreases, T_d approaches the lower horizontal asymptote (T_{cp}) which indicates the degree winter-time of reduction in growth. T_{mid} is the inflection point, indicating the temperature at which T_d is midway between the asymptotes. T_{sc} is a scale parameter at which T_d reaches roughly three-quarters of the distance between the asymptotes. We calculated average daily temperature based the thermometer we buried in the soil. Because there were no measurements available from day 1 to day 57, we assigned to these days a temperature of 22.46°C averaging the soil temperature during the same period of time in the second year.

Daily biomass gain is taken to be an asymptotic function of light availability. As light availability approaches 100% (full daylight), L_d approaches 1:

$$L_d = 1 - \exp[\log 2 \times (L_{\min} - L_{obs}) / L_{0.5}] \qquad \text{(Eq. 5)}$$

where L_{min} indicates the light compensation point (the minimum amount of light needed to maintain carbon balance). $L_{0.5}$ represents the light level at which L_d = 0.5, and thus indicates low-light growth efficiency . We assigned 3, 17, 44, 100 as observed percentages of light to low-, medium-, high- and full-light treatments.

Now RGR can be calculated by combining equations 1 and 3:

$$RGR = C_{i,d} / M_{i,d} = T_{i,d} \times L_{i,d} \times G0_i \times M_{i,d}^{\beta_i - 1} \qquad \text{(Eq. 6)}$$

RGR calculated in this way is corrected for plant biomass, thus in the following paragraphs we referred to it size-standardized RGR (SGR).

Parameter estimation

The model required the estimation of seven parameters: $G0$, β, T_{cp}, T_{mid}, T_{sc}, L_{min} and $L_{0.5}$. To define the model and estimate these parameters, we used "Filzbach", a packaged C library (Turnbull et al. 2008), which applies Markov Chain Monte Carlo (MCMC) methods to generate a posterior distribution for each parameter given model and the data. Bayesian posterior estimates numerically resemble much the estimates from maximum or restricted maximum likelihood methods (Kéry, 2010, Link & Barker, 2010), but they are exact rather

than approximate, because they account for the full uncertainty in the modeled system (Gelman & Hill, 2007). We ran the model for sufficient iterations (up to 200,000) that the likelihood of the parameters, given the model and data, were constant. The uncertainty in the parameter estimate was evaluated using the posterior distribution of this parameter. We report here the mean and 95% Bayesian credible interval for each parameter (analogous to a 95% confidence interval in classical statistics) in Table 2.

To determine the degree to which each parameter varied among species, we compared the Bayesian information criterion (BIC) (Schwarz, 1978) from model fits where the parameters were made species-specific or global. We chose BIC as the criterion for model selection as BIC yields more parsimonious models for large datasets than does AIC (Burnham & Anderson, 2002). We began with a model in which all seven parameters were species-specific, and then fitted models with each parameter in turn made global. All of these models had lower BICs compared with the fully species-specific model. From the set of the seven reduced models we selected the one with the lowest BIC and set the relevant parameter to be permanently global. We then fitted the six possible models with a second global parameter. From these six models we again chose the one with the lowest BIC, fixing the corresponding global parameter, and so on until the BIC of the selected model no longer decreased. The resulting model was then used as the most parsimonious fit.

Data analysis

Univariate analyses of variance

We conducted analyses of variance (ANOVA) to evaluate the influences of age, light, leaf habit (deciduous versus evergreen species), species identity, and their interactions SLA, LMR, SMR, RMR and NAR. Species and interactions involving these terms were considered as random terms and used to construct appropriate F-ratios for significance tests. Due to the complexity of the design with the crossed effects of age, light and species, we tested each term manually against the correct error term as in classical mixed-model analysis of variance (Green & Tukey, 1960). For all analyses, the functional traits were natural log-transformed to increase homoscedasticity of residuals and to decompose SGR

into the three functional traits as its components (see Eq. 1). The statistical analyses were calculated with the software GenStat 13th edition (Payne, Murray, Harding *et al.*, 2009). For gas-exchange and chemical traits which were measured only during and after the final harvest in July 2009, the explanatory factors were light, leaf habit and their interaction.

The three functional traits as components of SGR

We used a variance decomposition method to tackle the relationships between SGR and SLA, LMR and NAR as its components and calculated the contribution and importance of each of them to the variance in ln(SGR) (Rees *et al.*, 2010). We chose this method because a simple correlation test between RGR and the three functional traits is not appropriate due to the fact that the functional traits are components of SGR as shown in equation 1 (Wright & Westoby, 2001). To sum up the method in brief, the variation of sgr can be expressed as follows:

$$\begin{aligned} \mathrm{Var}(\mathrm{sgr}) = {} & \mathrm{Var}(\mathrm{nar}) + \mathrm{Cov}(\mathrm{nar}, \mathrm{sla}) + \mathrm{Cov}(\mathrm{nar}, \mathrm{lmr}) \\ & + \mathrm{Var}(\mathrm{sla}) + \mathrm{Cov}(\mathrm{nar}, \mathrm{sla}) + \mathrm{Cov}(\mathrm{sla}, \mathrm{lmr}) \\ & + \mathrm{Var}(\mathrm{lmr}) + \mathrm{Cov}(\mathrm{nar}, \mathrm{lmr}) + \mathrm{Cov}(\mathrm{sla}, \mathrm{lmr}), \end{aligned} \qquad \text{(Eq. 7)}$$

Where Var stands for the variance, Cov stands for the covariance, and lowercase of characters to indicate natural log-transformed traits. The sum of each line can be interpreted as contribution of this component to the total variation of sgr (we noted it as Cont∗). Cont∗ thus can be both positive and negative due to the sign of covariance. However, the negative covariance can lead to an underestimation of the contribution. Thus besides calculating Cont*, we also used the absolute values of the covariance terms in the equation mentioned above . We divided the sum by a constant, C, the sum of absolute value of the terms on the right-hand side of equation 7 so as to make the contributions of each components sum to 1. So, for example, the contribution of sla can be written as

$$\mathrm{Cont}(\mathrm{sla}) = \frac{\mathrm{Var}(\mathrm{sla}) + |\mathrm{Cov}(\mathrm{nar}, \mathrm{sla})| + |\mathrm{Cov}(\mathrm{sla}, \mathrm{lmr})|}{\mathrm{C}}. \qquad \text{(Eq. 8)}$$

Estimates of the variance-covariance matrix of the rgr components are sensitive to outliers, therefore we discarded data larger or smaller than 95% of the trait distribution of rgr and each component.

As NAR was calculated following equation 2, the positive relationship between SGR and NAR could be purely induced by calculation. Thus, we chose half of the plants for predicting SGR, and the rest for calculating NAR, SLA and LMR. In this way, SGR and NAR were calculated from independent datasets respectively. Both of the datasets contained all of the species×light combinations and similar plant number within each treatment. The total number of plants used in these two datasets were 232 and 229, respectively.

We refer to the above analysis as time-standardized analysis because growth components were directly calculated from the measurements of leaf mass, leaf area and plant mass; and SGR was predicted at the same date of harvest. To find out whether the contributions of growth components depend on plant biomass, we conducted the same analysis at a common plant biomass. We used the 25th percentile of the distribution of plant biomass at each harvest as the reference size, which was 2.29 g for the first-year seedlings and 20.23 g for the second-year seedlings. We selected these sizes because, at harvest times, all species×light combinations exist at these sizes. We estimated both leaf mass and leaf area at the reference size using regressions between leaf area, leaf mass and total plant mass (R^2>0.87). We predicted SGR for each species under each light treatment at both reference sizes using the selected growth model, with an average temperature (24°C) on the days of harvest (day 351 and 677) as the reference temperature. We refer to this analysis as size-standardized analysis because growth components and SGR were size-standardized (they were calculated at the same plant biomass). It worth noting that the SGR used in time-standardized analysis was also size-standardized but calculated at different plant biomass.

Results

Growth model selection and model-data comparison

The most parsimonious model had three global parameters (G_0=0.083, T_{cp}=0.025 and T_{sc}=0.478) and four species-specific parameters (β, $L_{0.5}$, L_{min}, T_{mid}) (model comparison see

Appendix A). The model fit well, as predicted species-mean biomass was closely correlated with the observed species-mean biomass at all light levels with R^2=0.94, 0.83, 0.85, 0.86 under 3%, 18%, 46% and 100% light, respectively (Appendix B).

β is a scaling parameter in the power-law function, indicating how much log (daily carbon gain) would change if log(plant mass) change for 1 unit when other parameters kept constant. β ranged from 0.257 (Pz) to 0.865 (Ch) and was always significantly less than one, indicating that growth slowed with increasing biomass for all species. This confirms that the choice of a power-law instead of an exponential growth model was necessary. β had greater value in deciduous than in evergreen species ($\beta_{\text{deciduous}} = 0.71$, $\beta_{\text{evergreen}} = 0.49$; p=0.009), which meant SGR decreased with growing plant size more rapidly in evergreen than in deciduous species (Fig. 2). Growth rates of evergreen species can exceed those of deciduous ones when plants were small (Fig. 2). The advantage of high growth rate at small plant size may explain the common observation that evergreen species predominate among the trees which occupy the shaded stratum of tropical and subtropical forests.

Both parameters describing growth responses to light were species-specific, showing species differed in their responses to light availability. $L_{0.5}$, the percentage of light at which half of the maximum daily carbon was obtained, ranged from 0.47% (Pz) to 37.9% (Co) with a mean value of 5.5%. L_{min}, the parameter indicating whole-plant light compensation point and the degree of shade tolerance of species, ranged from 0.023% (Ca) to 6.15% (Pf) with a mean of 0.24%. There was no difference between evergreen and deciduous species in L_{min}. The L_{min} of most species were rather similar and could not be distinguished by 95% Bayesian credible interval of the posterior distribution.

Two of the three parameters describing growth responses to temperature were global, which indicated that plant responses to temperature were similar. T_{mid} ranged from 15.7ºC (Ca) to 25.1ºC (Co) with a mean of 22.4ºC (parameter estimation see Table 2).

Influence of light, species identity and plant biomass on SGR

SGR generally increased with increasing light availability, until it reached a constant level (Fig. 1). At 2.29g, species SGR ranged from 0.36 (Co) to 44 mg g^{-1} day^{-1} (Arc) under 3% of light, and from 5.7 (Co) to 67 mg g^{-1} day^{-1}(Ts) under 100% light. At 20.23g, SGR was smaller, which ranged from 0.14 (Co) to 18 mg g^{-1} day^{-1} (Ts) under 3% of light and from 2.3 (Co) to 46 mg g^{-1} day^{-1} (Ch) under 100% of light. The evergreen species Pz and Co showed only a weak increase of SGR along the gradient of increasing light. Some species (e.g. Pf, Lc and Alc) exhibited negative SGR at low light (<10% of full light), in accordance with their high L_{min} (Table 2). For both sizes, evergreen and deciduous species had similar SGR at low light, but at high light (>50% of full light) evergreen species had generally lower SGRs than the deciduous species. There were changes in the rankings of species with increasing light level (Fig. 1).

The interspecific response curve of SGR on plant size exhibited large differences under 3% and 17% daylight (Fig. 2); the response curves under 44% and 100% of daylight were almost identical to the one under 17% of light and are thus not shown in the figure. The SGR of all the species decreased with increasing plant biomass and there were greater variations in SGR at smaller than at larger plant size, regardless of light availability. There were also changes in the rankings of species-specific growth rates with increasing plant size, but these changes were smaller than those between the lowest and the other light levels. Thus, SGR was influenced in complex ways by light availability, species identity and plant size.

Factors influencing morphological, chemical and physiological traits

SLA varied 5.7, 4.8, 3.2, 4.2-fold among species at 3, 17, 44, 100% of full daylight, respectively. Within species, the SLA of 1-year old plants varied 2.0–11.4 fold while that of 2-year old plants varied 1.6–9.5 fold. SLA was significantly influenced by plant age, light level, species leaf habit and species identity (Table 3). The overall mean of SLA decreased from year one (August 2008) to year two (July 2009), and decreased with increasing light availability (Fig. 3a). Deciduous species generally had higher SLA than

evergreen species at 3 and 17% of light, reflecting their thinner and more productive leaves in the low light. The difference between these two groups of plants became indistinguishable at higher light. Thus SLA in deciduous species decreased more rapidly with increasing light availability than that in evergreen species (Fig. 4; significant light × leaf habit interaction for SLA in Table 3).

Biomass allocation was influenced by light, seedling age, species identity and leaf habit groups in a complicated way. LMR, SMR and RMR had a variation of about 2-fold among species under each light treatment. In both years, the proportion of biomass allocated to belowground (roots) decreased with increasing light availability (Fig. 4). However, there was no consistent trend in the biomass partitioning in leaves and stems along the light gradient (Table 3). In general, evergreen species allocated more biomass to leaves comparing to deciduous species. For allocation to stems or roots, there were no differences between leaf habit groups (Table 3, Fig. 4).

The average NAR was lower in the second year (Fig. 3). NAR was generally increasing as light availability increased except for Pz (Fig. 4) and there was no significant difference between evergreen and deciduous species (Table 3). The difference between species was not significant (Table 3), although some deciduous species (e.g. Ch and Ts) showed higher NAR under 100% light (Fig. 4; species mean of SLA, LMR and NAR are shown in Appendix C).

Across all species, N_{mass} varied 4.2-, 3.9-, 3.2-, 3.2-fold from low to high light treatments. The mean N_{mass} was higher in deciduous (2.9% ± 0.7%) than in evergreen species (2.2% ± 0.6%). N_{mass} slightly decreased with higher light ($p=0.047$), which was mostly incurred by the responses of deciduous species. N_{area} varied 2.1-, 1.9-, 2.2, 2.9-fold from low to high light treatments. N_{area} in leaf habits were not different and both strongly increased with light ($p<0.001$) (Fig. 5). Leaf thickness (T) increased with increasing light availability, and there was no difference between the two leaf habits (Table 6; Fig. 5)

In general, A_{mass}, gs_{area} and PNUE had greater values in deciduous than evergreen species (Fig. 5) across all the light treatments. A_{area} and gs_{area} increased from low to high light in both evergreen and deciduous species, while A_{mass} decreased for deciduous species and stayed unchanged for evergreen species. A_{area} in deciduous species showed an

asymptotic response to increasing light: it increased rapidly from low light (3%) to medium light (17%), kept on increasing with less acute rate to high light (44%) and stayed relatively constant from high to full light. In evergreen species A_{area} showed different response: there was hardly increase of A_{area} between low and medium light, then it was followed by a linear increase from medium to full light. Light compensation point (LCP) had similar values in deciduous and evergreen species under 3% and 17% light, while deciduous species had much higher LCP under 44% and 45% (Fig. 5).

The difference between deciduous and evergreen species are large concerning gas-exchange traits. The only exception was the evergreen Pf, which had gas-exchange characteristics similar to deciduous species and morphological traits as found in evergreen species.

The influences of the three growth components on SGR

Comparing to SLA and LMR, NAR made the greatest contribution to SGR (ranging from 0.51 to 0.73) in both time-standardized and size-standardized analyses, and under all light conditions (Fig 6). SLA had less contribution but still positive contribution to SGR whereas LMR had the least and negative contribution to SGR (Figs 6 and 7).

In time-standardized analysis, NAR had strong positive correlation with SGR under six out of the eight age×light combinations (Table 4; Fig. 7(c) and 7(f)). In August 2008, the NAR-SGR shared common SMA slope of 1.19, while in July 2009, the slopes were increasing as light availability increased, which were 0.63 for 3% of light, 0.78 for 44% of light and 1.17 for 100% of light. SLA and LMR hardly had any correlation with SGR (Table 4; Figs 7(a), 7(b), 7(d) and 7(e)). In size-standardized analysis, NAR again had strong positive correlations with SGR (Table 4; Figs. 7(i) and 7(l)). They were significant under all of the eight light×size combinations and shared a common slope of 1.1 for 2.29g plants and 0.93 for 20.23g plants. The elevations of these paralleled SGR–NAR relationships were generally lower at higher light availability. It meant for a certain SGR, NAR was higher in the light than in the shade. SLA was positively related to SGR under seven out of the eight combinations in size-standardized analysis (Table 4; Fig. 7(g) and

7(j)). For 2.29g plants, these correlations shared a common slope of 2.64, while for 20.23g plants, the slopes were indistinguishable between 3% and 100% of light (slope = 2.65) and under 44% of light the slope was 4.8. The elevations of the paralleled SGR–SLA relationships increased with increasing light availability, so that for a certain SGR, plants had smaller SLA under higher light conditions. LMR was rarely related to SGR except for one out of the eight light×size combinations (Table 4, Figs 7(h) and 7(k)).

Gas-exchange and chemical traits in relation with SGR

A_{mass} was positively correlated with SGR (for 20.23g plants) at 17% (r=0.79, p=0.002) and 44% light (r=0.72, p=0.01). N_{mass} was also positively correlated with SGR at 3% (r=0.67, p=0.01), 44% (r=0.64, p=0.05) and 100% light (r=0.56, p=0.03). Traits on an area base rarely correlated with SGR. The only significant case was SGR–A_{area} at 17% light (r=0.8, p=0.01) (Fig. 8).

Discussion

We examined the responses of leaf morphology, physiology, biomass partitioning as well as size-standardized relative growth rate to a light gradient among 14 subtropical species over two years. We tested it at two sequential years and at two plant common biomass because plants commonly show ontogenetic changes over time. We found that multiple factors drive differences in relative growth rate in contrasting irradiance, among which ontogeny and leaf habit were of special importance.

Benefit of our approach

In traditional analysis of growth, RGR are calculated directly from observations representing growth rate for this time interval assuming RGR stays constant over period of growing (Hunt, 1982) Our study provided evidences for the influences of plant size, temperature, light and their interactions on plant growth (Figs. 1 and 2; Table 2 showed one parameter of temperature effect was species-specific). Thus estimating RGR over a period

of time can not precisely reflect the status of plants at a certain moment, especially when there is a long interval between harvests.

In a same sense, traditionally NAR is also estimated over a period of time following the formula provided by Williams (1946):

$$NAR = \frac{W_2 - W_1}{T_2 - T_1} * \frac{\log L_{A_2} - \log L_{A_1}}{L_{A_2} - L_{A_1}}.$$

However in this formula, leaf turnover was not included. It can well be used to approximate the real NAR of plants in a short time study (several weeks) with species rarely shed their leaves during the study, but can bring errors into studies spanning over years, especially with a mixture of deciduous and evergreen species as it was in the current study. To overcome this difficulty, we used species-specific growth model so that to estimate the instantaneous RGR and NAR (daily biomass gain divided by the total leaf area) on a specific day. Armed with this novel approach, our results are more reliable. Variation in net assimilation rate (NAR) explained the largest amount of variation in SGR, SLA had the second biggest contribution while biomass allocation had the least (negative) importance. This result was obtained when SGR was calculated with a mechanistic model (Eq. 6) which used only daily increases of plant size and daily temperature and light as inputs (Turnbull *et al.*, 2008). NAR was calculated from this measure of SGR, but to avoid spurious correlations in the subsequent analyses, different individual replicates were used for SGR and NAR.

Traits determining SGR

Among the three growth components (SLA, LMR and NAR), we found NAR explained the most variation in SGR among seedlings of the 14 subtropical woody species irrespective of light availability, plant age or biomass, i.e. fast growing species always had high net assimilation rate. SLA was also positively correlated with SGR when species were compared at a common plant biomass. In previous studies, some found plant and leaf morphology are more important than physiological activities, suggesting fast-growing species achieve a higher growth rate mainly because they develop relatively more leaf area

per leaf mass or per plant mass and physiological activity expressed per unit leaf area seems only of secondary importance (Poorter *et al.*, 1990, Poorter & Van der Werf, 1998), whereas some other studies found the opposite (Quero, Villar, Maranon *et al.*, 2008, Shipley, 2006, Walters, Kruger & Reich, 1993a). It has also been suggested that the relative importance of NAR and SLA on SGR differ among light environments (Poorter, 1999, Shipley, 2002, Meziane *et al.*, 1999) and continuously change with size (Walters *et al.*, 1993b) or time (Villar *et al.*, 2005). Nonetheless, studies using woody plants as research objects usually showed physiological activities are important, as shown in the present study (Lin, Harcombe, Fulton *et al.*, 2002, Portsmuth *et al.*, 2007, Walters *et al.*, 1993a, Quero *et al.*, 2008, Shipley, 2006) (but see also Poorter, 1999). Different plant type may be responsible for the inconsistency found in previous studies. One important difference between woody species and herbaceous species is the type of leaf demography: in herbaceous species leaves are produced at the same time as stems and branches whereas in woody species new leaves can be produced repeatedly on the persisting structure of stem and branches. Thus, in woody species, leaves in all parts of the plant can be produced simultaneously and according to the local light conditions. In herbaceous species, however, leaves are produced from the bottom up and inside out and thus exposed to continuously changing local light conditions as older leaves are overtopped by newer ones. This challenges herbaceous plants to continuously adjust the leaf functional traits (Schmid & Bazzaz 1994, Egli & Schmid 2000).

We suggest analysis without considering the variation in plant biomass can also be a source of bias, because both SGR and functional traits change as plants grow bigger (ref) and the relationships between SGR and plant biomass are not parallel but species specific (Fig. 2). Thus plant biomass is a confounding factor in the analysis of growth–trait relationships. For example, we found when compared at the same plant biomass, SLA also positively related to RGR and it was robust across light treatments. However, when plant biomass is not corrected in the analysis, SLA did not show any relation with growth (Fig. 7).

None of the partitioning variables were correlated with relative growth rate, suggesting biomass allocation was not an important factor determining plant growth rate.

Surprisingly, some species with a high LMR even had lower RGR than species with low LMR (Fig. 7), which is opposite to previous observations (Poorter *et al.*, 1990, Poorter *et al.*, 1998). However, it was mainly due to the interdependence among traits which was also found previously (Meziane *et al.*, 1999, Poorter, 1989). In the analysis of partial correlation, LMR appeared to be positively correlated to RGR when NAR was fixed, while the relationship was unclear or negative when SLA was fixed (Table 5). It indicated the covariation between LMR and NAR was the key to explain the negative relationship between LMR and RGR under certain light conditions.

We found N_{mass} was positively related to SGR in three out of the four light treatments, while N_{area} was not related to SGR in any treatment. This finding was consistent with previous studies. Cornelissen *et al.*(1997), for example, studied seedlings of 81 woody species from the cool-temperate zone of western Europe and found leaf nitrogen expressed on a mass base, not on an area base, was positively correlated with mean relative growth rate. photosynthetic capacity is also a good indicator of plant growth potential.

Light-use strategy in seedlings

In high light environments, there were 10- to 20-fold variation in SGR and 2- to 6-fold variation in functional traits across the 14 woody species that all occurred in the subtropical forest in our study. The trend in SGR, morphological and physiological trait and species ecology were consistent with theories on resource availability, growth and carbon balance strategies (Bazzaz, 1979, Grime, 1979). Species which are commonly found under high-light environment in the forest (e.g. Ch in deciduous species and Pf in evergreen species) had suppressed growth at low light, gained growth rapidly once light availability increased and obtained rather high growth rate at high light. This strategy was associated with traits beneficial of growth such as high photosynthetic rates, high leaf nitrogen and high SLA. On the other end of the strategy spectrum there are species with low potential rate of light capture so they are not able to maximize short-term carbon gain rate, but they manage to maintain positive net carbon gain under adverse environments such as the deeply shaded understory in which late successional species are commonly found (Walters

& Reich, 1999). This was supported by the low growth rate, low photosynthetic rates, low SLA and high lamina thickness of late successional species. However, there was no tendency for species placed along a light-use strategy continua to have different allocation patterns (Fig. 4), which was in contrast to the findings in Walters *et al.* (1993a) and Kitajima (1994). In other words, allocation pattern was not selected to cope with light stress in the shade. Previous studies suggested that shade intolerant, early successional species had high root mass ratio and low leaf mass ratio and vice versa (Kitajima, 1994, Walters *et al.*, 1993a). In our study, in the opposite, leaf mass ratio was higher in late or intermediate successional, shade tolerant evergreen species than early successional deciduous species (Fig. 4). However, after predicting LMR at a common plant biomass, LMR was no more distinguishable between these two leaf habits. Thus we conclude that the observed difference in biomass allocation between functional types is simply due to difference in plant biomass as suggested in allometry theory : when plants grow bigger, the relative allocation to leaf tends to decrease and that to root tends to increase. Our results showed biomass allocation is not an important aspect concerning light-use strategy of plants. Rather, allocation pattern may be involved in cope with water stress (Engelbrecht, Comita, Condit *et al.*, 2007) and the patchiness of soil minerals.

Despite interspecific difference, there is a general trend in which plants respond to shade. We found for all species, the deleterious effect of shade was compensated by enhanced SLA (Fig. 4) and an increase in NAR was induced by increasing light availability due to a higher rate of photosynthesis per unit leaf area. Those results were in consistence with previous studies (Givnish, 1988, Konings, 1989). There was also evidence of increasing allocation to root when light is not the limiting resource as suggested by the theory of “functional equilibrium” (Brouwer, 1962), while allocation to leaf was largely unaffected by light (Reich, Tjoelker, Walters *et al.*, 1998, Poorter *et al.*, 1998). This results stayed valid when species were compared at a common plant biomass.

Conclusions

What determines the large variation of growth and how light, seedling biomass, functional groups interfere in the question was explored in this paper. Armed with mechanistic approach, we were able to estimate standardized relative growth rate (SGR) and net assimilation rate (NAR) at the exact time point of traits being measured, different from the traditional approach of assuming SGR stays constantly through plant development. We found light had strong influence on morphology of leaves, leaf- and whole-plant physiology, but only slightly on biomass allocation to roots. Between seedlings from different successional stages, We found NAR explained the most of variation in SGR, and the result didn't change under any light availability. Furthmore, Leaf nitrogen and photosynthetic capacity are also good indicators of plant growth potential. Specific leaf area (SLA) was positively correlated with SGR when compared at a common size, but not when size difference was not accounted for. Size largely influence traits and rates, showing size-standardized comparison is important. As the change of partitioning with changing size were not parallel between species, the choice of plant size (biomass) for comparison had critical influence on the results.

Tables

Table 1. Species name, family and growth forms. This nomenclature follows the "Flora of China" (ECCAS, 1974–1999)

Species name	Family	Short	Growth	Height	Successional
Deciduous					
Alangium chinense	Alangiaceae	Alc	shrubs/small trees	3–5m	Early
Aralia chinensis	Araliaceae	Arc	shrubs/small trees	1.5–7m	Intermediate
Castanea henryi	Fagaceae	Ch	trees	up to30m	Early
Choerospondias axillaris var. *pubinervis*	Anacardiaceae	Ca	trees	8–20m	Intermediate
Diospyros kaki var. *silvestris*	Ebenaceae	Dk	trees	up to 27m	Intermediate
Rhus punjabensis	Anacardiaceae	Rp	shrubs/trees	2–10m	Early
Toxicodendron succedaneum	Anacardiaceae	Ts	trees/small trees	1–10m	Intermediate
Evergreen					
Camellia oleifera	Theaceae	Co	shrubs/trees	1–7 m	Intermediate
Diospyros cathayensis	Ebenaceae	Dc	trees	up to10m	Intermediate
Lindera communis	Lauraceae	Lc	shrubs/trees	1–5m	Early
Lindera limprichtii	Lauraceae	Ll	trees	10m	Intermediate
Phoebe microphylla	Lauraceae	Pm	trees	10m	Intermediate
Phoebe zhennan	Lauraceae	Pz	large trees	up to 30m	Late
Pyracantha fortuneana	Rosaceae	Pf	shrubs	3m	Early

Table 2. Species-specific parameter estimation from selected 3-p model (Global parameter G_0=0.083, T_{cp}=0.025,T_{sc}=0.478). The first seven lines represent deciduous species and following seven lines represent evergreen species.

	β			$L_{0.5}$			L_{min}			T_{mid}		
	L95	mean	U95	L95	mean	U95	L95	mean	U95	L95	mean	U95
Alangium chinense	0.586	0.736	0.871	1.269	2.371	4.552	0.178	1.136	1.907	19.419	22.233	22.906
Aralia chinensis	0.454	0.585	0.705	1.070	1.418	1.825	0.000	0.111	0.742	16.492	21.425	22.840
Castanea henryi	0.711	0.865	0.998	13.645	17.844	23.609	0.127	1.214	2.009	22.358	23.155	23.653
Choerospondias axillaris	0.525	0.615	0.736	3.688	7.967	12.378	0.001	0.023	0.106	12.031	15.729	20.137
Diospyros kaki	0.520	0.755	0.975	1.784	3.177	5.167	0.046	1.114	2.222	23.089	23.562	23.953
Rhus punjabensis	0.497	0.604	0.752	2.596	4.347	6.280	0.002	0.127	0.554	16.643	21.284	22.453
Toxicodendron succedaneum	0.674	0.794	0.920	1.015	9.705	13.859	0.027	0.364	2.338	21.931	22.575	22.898
Camellia oleifera	0.172	0.587	0.939	16.290	37.976	91.679	0.001	0.053	0.286	24.342	25.074	25.973
Diospyros cathayensis	0.169	0.388	0.634	3.142	5.614	9.438	0.001	0.040	0.170	21.423	22.704	23.212
Lindera communis	0.343	0.590	0.842	1.458	2.769	4.307	2.197	2.586	2.833	22.250	23.041	23.451
Lindera limprichtii	0.186	0.453	0.776	4.894	7.157	9.635	0.001	0.727	1.772	22.655	23.353	23.921
Phoebe microphylla	0.208	0.453	0.741	5.396	9.912	15.112	0.001	0.044	0.210	22.304	23.151	23.636
Phoebe zhennan	0.108	0.257	0.529	0.160	0.470	0.949	0.000	0.137	0.830	23.461	24.497	25.463
Pyracantha fortuneana	0.534	0.699	0.863	5.526	8.101	12.479	5.397	6.146	7.301	21.507	22.701	23.095
grand mean	0.341	0.578	0.811	2.571	5.491	10.596	0.041	0.242	0.819	19.942	22.423	23.874
grand sd	0.175	0.391	0.671	0.726	1.136	1.824	1.569	2.640	4.060	0.049	0.120	0.247

Table 3. ANOVA for the effect of age (351 and 677 days), light (3%, 17%, 44% and 100%), species leaf habit (evergreen versus deciduous), species identity, shade house/full-light quadrate identity and interactions on specific leaf area (SLA), leaf mass ratio (LMR), stem mass ratio (SMR), root mass ratio (RMR) and net assimilation rate (NAR). df: degrees of freedom, *F*: variance ration, *P*: type-I error probability). SLA and NAR were log transformed to obtain normality.

	SLA			LMR		SMR		RMR		NAR		
	df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	Error term
Age	1	29.046	<0.001***	1.465	0.249	9.780	0.009**	2.154	0.168	26.339	<0.001***	Age.Species
Light	3	14.897	<0.001***	2.162	0.132	0.998	0.419	15.040	<0.001***	6.239	0.005**	House
House	16	2.636	0.001***	1.488	0.107	2.002	0.014*	0.831	0.650	2.239	0.005**	House.Species
Leaf habit	1	10.400	0.007**	11.164	0.006**	2.675	0.128	4.019	0.068	2.770	0.122	Species
Species	12	2.922	0.006**	4.818	<0.001***	8.238	<0.001***	6.176	<0.001***	1.347	0.236	Light.Species
Age.Light	3	3.192	0.035*	7.043	0.001***	12.671	<0.001***	0.032	0.992	1.993	0.133	Age.Light.Species
Age.Leaf habit	1	0.017	0.899	1.304	0.276	0.004	0.952	2.425	0.145	2.573	0.135	Age.Species
Light.Leaf habit	3	4.795	0.007**	0.604	0.617	0.807	0.499	1.206	0.321	3.154	0.036*	Light.Species
Age.Species	12	1.344	0.239	2.001	0.055	1.488	0.175	2.879	0.007**	4.055	0.001***	Age.Light.Species
Light.Species	36	1.408	0.157	1.164	0.327	0.848	0.688	1.797	0.043*	2.190	0.011*	Age.Light.Species
Age.Light.Leaf habit	3	4.277	0.011*	0.129	0.942	0.142	0.934	0.371	0.774	2.406	0.084	Age.Light.Species
Age.Light.Species	35	0.674	0.911	0.899	0.631	1.166	0.265	0.985	0.502	0.706	0.882	Residual
House.Species	200	0.846	0.851	0.828	0.881	0.726	0.979	1.030	0.433	0.888	0.771	Residual
Residual	120											

Table 4. Relationships between RGR and growth components in the time-standardized and size-standardized analyses. L, M, H, O indicate 3%, 17%, 44% and 100% of full daylight treatment. Numbers show Pearson correlation coefficient (*:P <0.05, **: P <0.01, ***: P <0.001).

	Light	Common time		Common size	
	treatment	August 2008	July 2009	2.29g	20.23g
RGR-SLA	L	0.47	0.56	0.69**	0.85***
	M	0.51	-0.06	0.69**	0.18
	H	0.75**	0.35	0.83***	0.56*
	O	0.41	0.19	0.71**	0.71**
RGR-LMR	L	0.1	-0.66	-0.39	-0.31
	M	0.11	0.03	-0.49	-0.37
	H	0.03	-0.12	-0.58*	-0.34
	O	0.56*	0.39	-0.42	-0.4
RGR-NAR	L	0.79***	0.9***	0.95***	0.83***
	M	0.73**	0.48	0.91***	0.91***
	H	0.81***	0.8***	0.92***	0.96***
	O	0.24	0.55*	0.92***	0.95***

Table 5. Interspecific partial correlations between LMR and RGR at two plant size (2.29g and 20.23g), when either NAR or SLA is fixed. Treatments: L=3%, M=17%, H=44% and O=100% of full light; "All" includes all the light treatments.

	r(LMR,RGR/NAR)		r(LMR,RGR/SLA)	
	2.29g	20.23g	2.29g	20.23g
All	0.14	0.58***	-0.35*	-0.24
L	0.15	0.93***	-0.18	-0.58*
M	0.58*	0.43	-0.11	-0.39
H	0.72***	0.62**	-0.43	-0.30
O	0.70**	0.68**	0.12	-0.34

Table 6. Results of a two-way ANOVA for structural and physiological leaf traits, with light (L) and leaf habit (ED) as fixed effects. A_{area}= maximal rate of photosynthesis on an area basis (μmol CO_2 m^{-2} s^{-1}), A_{mass}= maximal rate of photosynthesis on a mass basis (nmol g^{-1} s^{-1}), N_{area}=leaf nitrogen content on an area basis (g m^{-2}), N_{mass}= leaf nitrogen content on a mass basis (%), gs_{area}=stomatal conductance (mmol m^{-2} s^{-1}), T=leaf thickness (mm), PNUE= photosynthetic nitrogen-use efficiency (μmol g^{-1} s^{-1}), LCP= light compensation point.

		A_{mass}		A_{area}		N_{mass}		N_{area}	
	Df	F	P	F	P	F	P	F	P
L	9.1	0.001***	9.1	17.1	<0.001***	3.2	0.047*	20.2	<0.001***
ED	61.2	<0.001***	61.2	91.8	<0.001***	6.9	0.024*	0.1	0.808
L×ED	4	0.018*	4	2.5	0.079	1.4	0.266	0.9	0.466

		gs_{area}		PNUE		LCP		T	
	Df	F	P	F	P	F	P	F	P
L	3	4.5	0.014*	6.3	0.008***	12.9	<0.001***	9.9	0.001***
ED	1	45.5	<0.001***	38.0	<0.001***	5.7	0.034*	0.1	0.93
L×ED	3	1.6	0.214	1.5	0.23	3.3	0.033*	0.3	0.82

Figures

Fig. 1: Estimated size-standardized relative growth rate (SGR) for each species in response to a light gradient from 3% to 100% of full light. SGR were estimated at plant biomass of (a) 2.29g and (b) 20.23g, respectively. Solid lines indicate deciduous species and dashed lines indicate evergreen species. The legend in detail is the same as in Fig. 2.

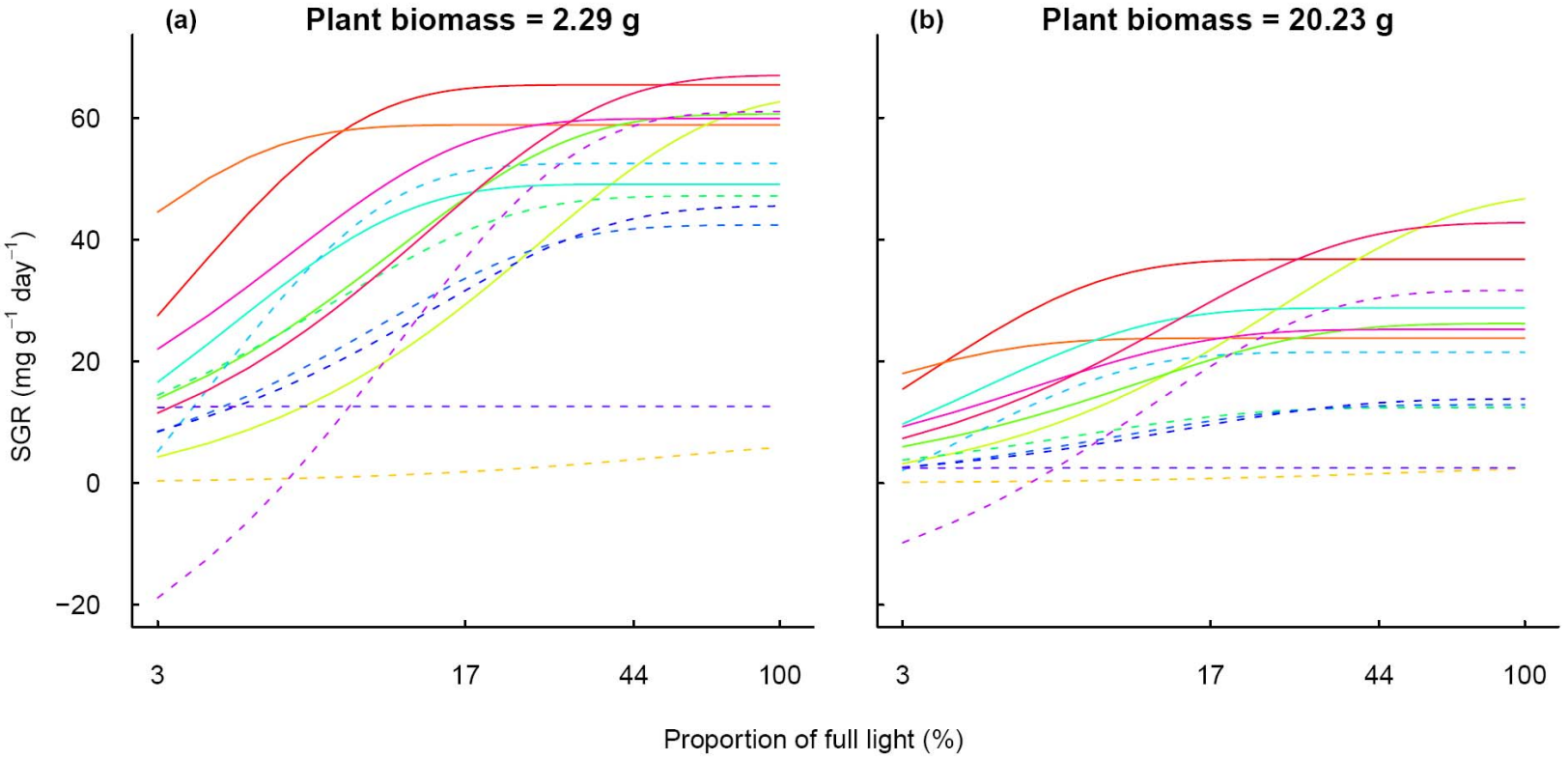


Fig. 2: Estimated size-standardized relative growth rate (SGR) for each species in relation to total plant biomass (0.1g–100g) at (a) 3% and (b) 17% full light. Figures for higher light availability were not shown as their shapes are similar to (b). Solid lines indicate deciduous species and dashed lines indicate evergreen species.

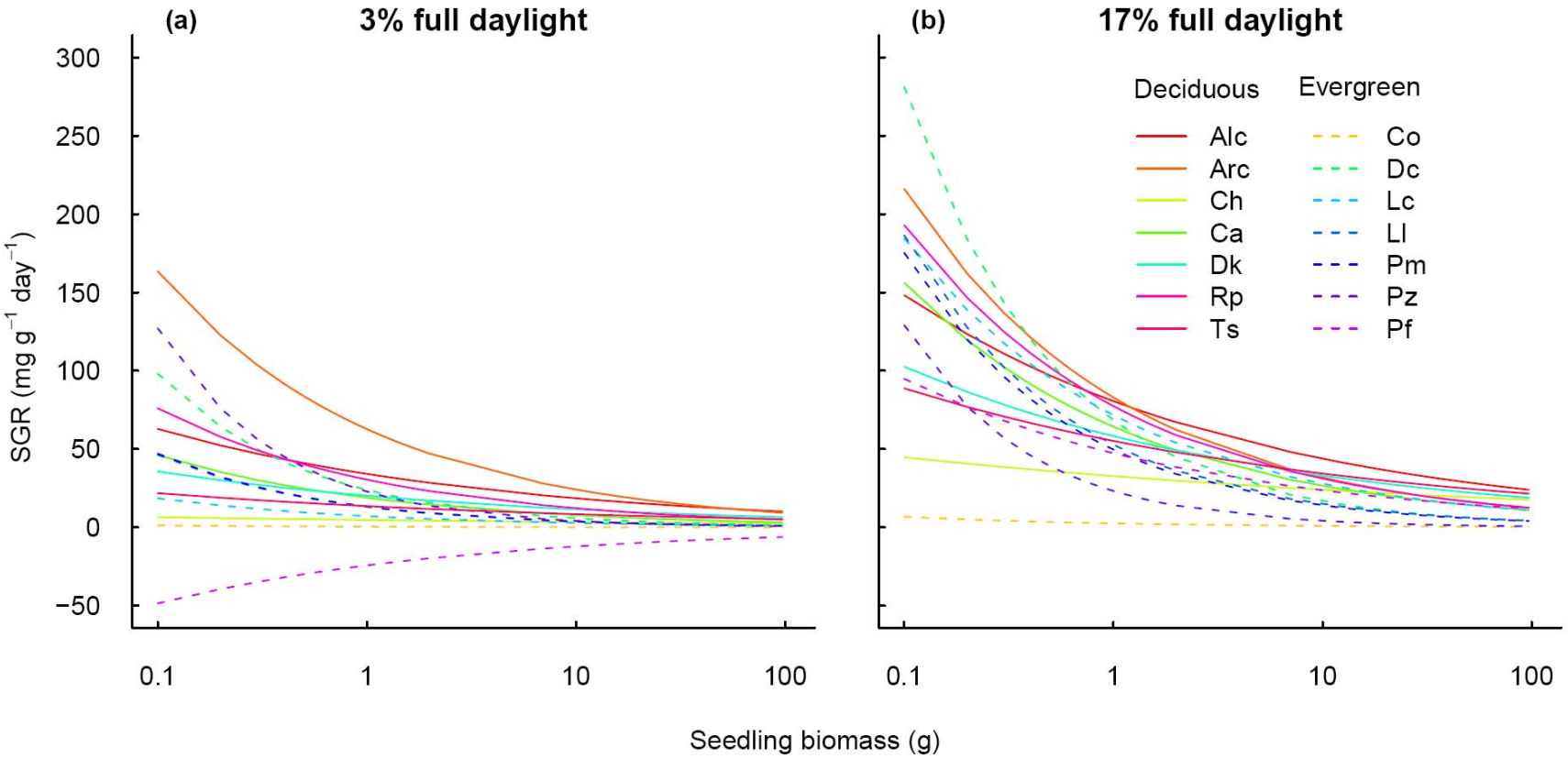


Fig. 3. (a)The average specific leaf area (SLA), (b) leaf mass ratio (LMR) and (c) net assimilation rate (NAR) subject to a light gradient of 3%, 17%, 44% and 100% of full daylight observed in August 2008 and July 2009. Error bars indicate standard error. Data points from July 2009 were slightly jittered to avoid overlapping.

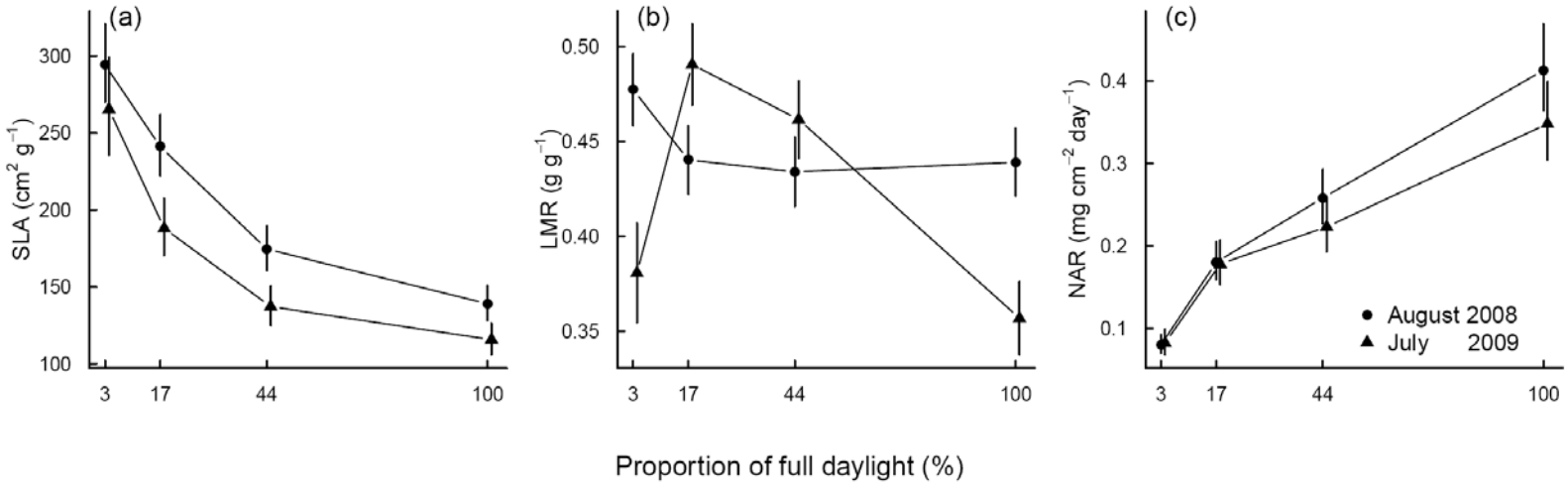


Fig.4. Species mean of specific leaf area (SLA), leaf mass ratio (LMR), stem mass ratio (SMR), Root Mass Ratio (RMR) and NAR (Net Assimilation Rate) in response to light level at different plant age. Trait values were predicted at a common plant biomass (2.29g for August 2008 and 20.23g for July 2009).

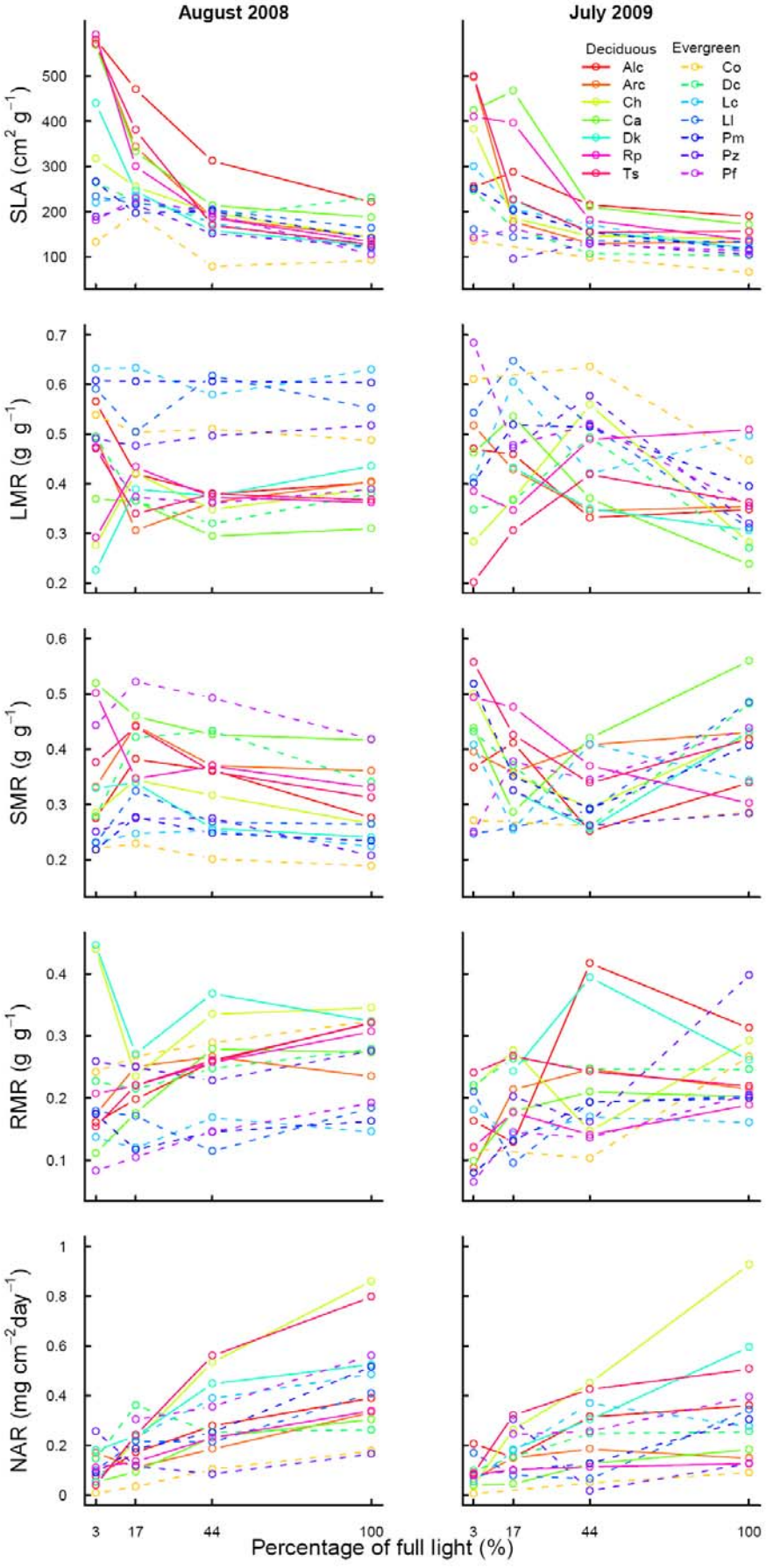

August 2008
July 2009
Deciduous
Alc
Arc
Ch
Ca
Dk
Rp
Ts
Evergreen
Co
Dc
Lc
Ll
Pm
Pz
Pf
SLA (cm^2 g^{-1})
LMR (g g^{-1})
SMR (g g^{-1})
RMR (g g^{-1})
NAR (mg cm^{-2}day^{-1})
3
17
44
100
Percentage of full light (%)

Fig. 5 Structural and gas-exchange traits in response to a gradient of light from 3% to 100% of light. Those traits are: A_{mass}= maximal rate of photosynthesis on a mass basis (nmol g^{-1} s^{-1}), A_{area}= maximal rate of photosynthesis on an area basis (μmol CO_2 m^{-2} s^{-1}), N_{mass}= leaf nitrogen content on a mass basis (%), N_{area}=leaf nitrogen content on an area basis (g m^{-2}), gs_{area}=stomatal conductance (mmol m^{-2} s^{-1}), PNUE= photosynthetic nitrogen-use efficiency (μmol g^{-1} s^{-1}), LCP= light compensation point (% of light) and leaf thickness (mm). Solid points indicate deciduous species and circles indicate evergreen species. Error bar shows standard error of the mean.

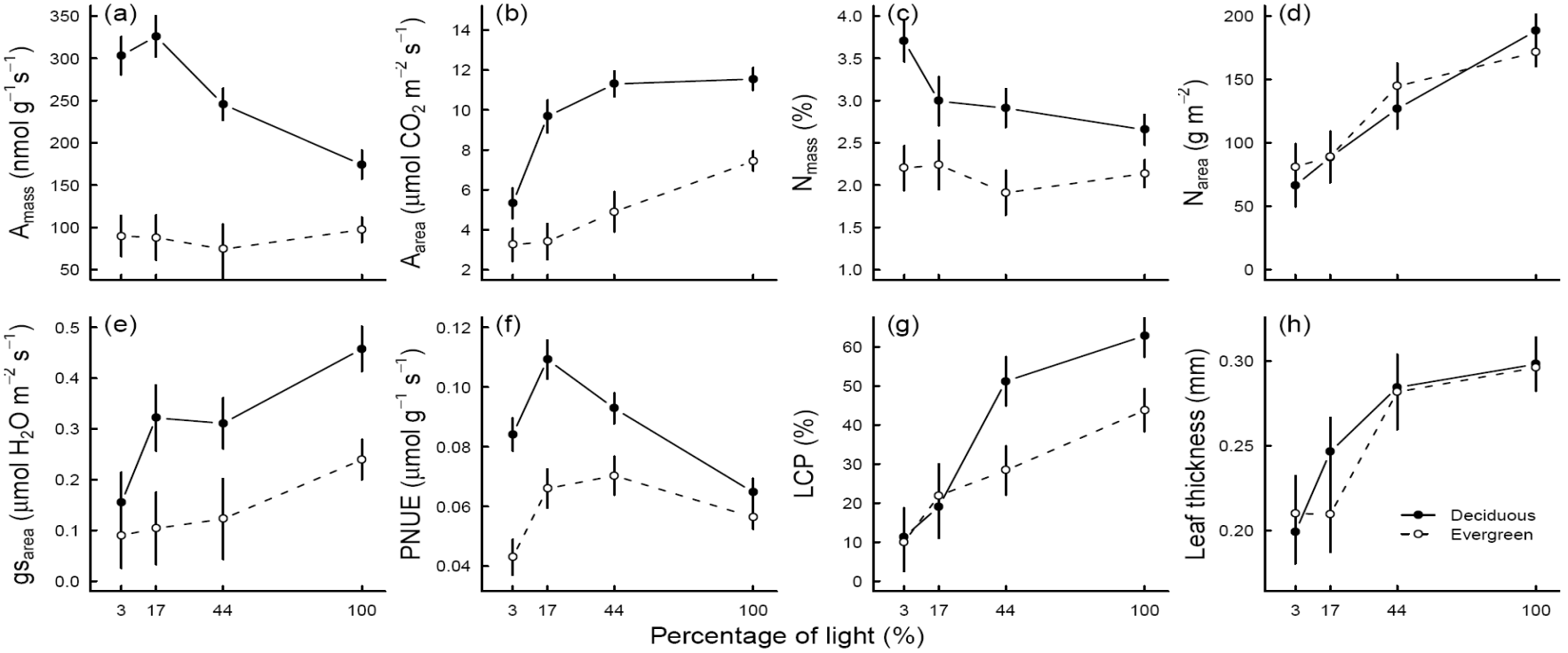


Fig. 6. Contribution of each growth component to RGR under 3, 17, 44 and 100% of full daylight. (a) and (b) show results from time-standardized analysis, (c) and (d) show results from size-standardized analysis. L=3%, M=17%, H=44% and O=100% of full light. LMR: leaf mass ratio. SLA: specific leaf area. NAR: net assimilation rate.

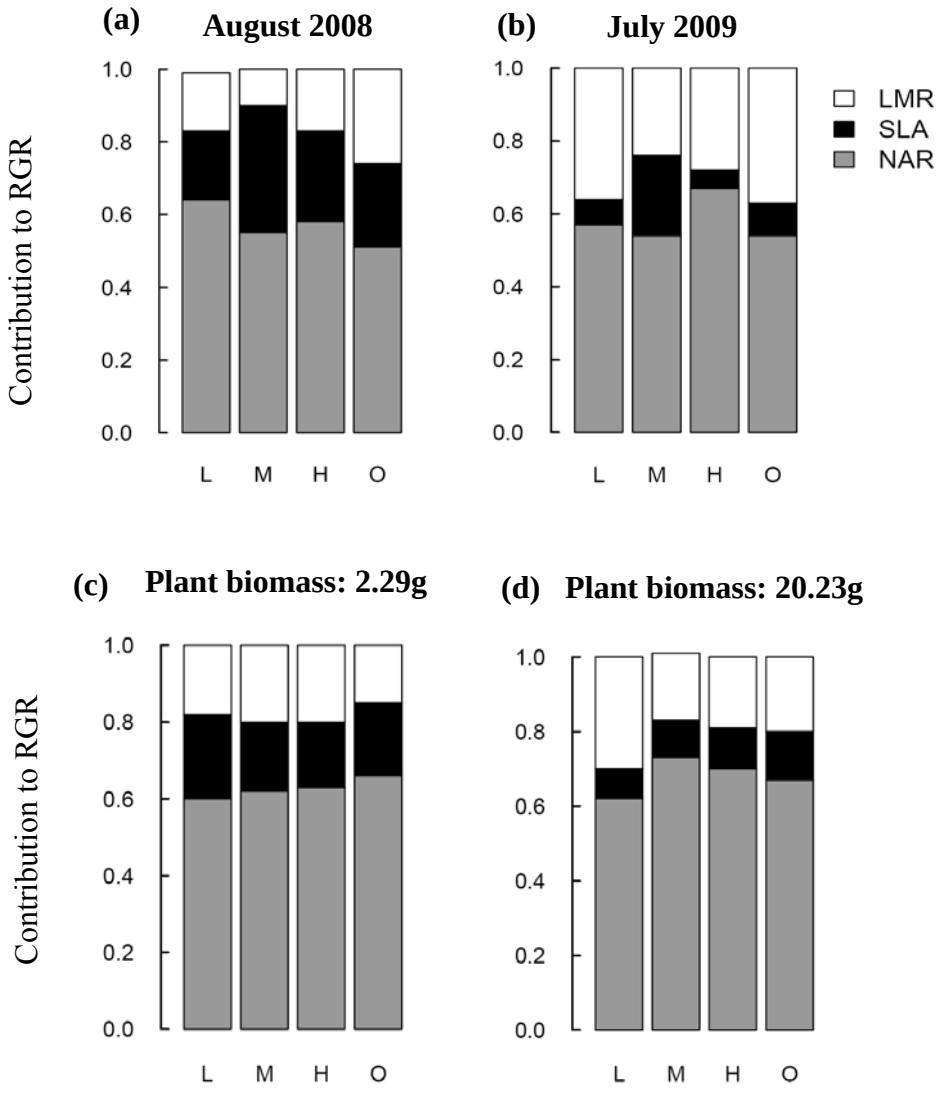


Fig. 7. Correlations between SGR and its components (SLA, LMR and NAR) using time-standardized analysis ((a)–(f)) and size-standard analysis ((g)–(l)). (a)–(c), August 2008; (d)–(f), July 2009; (g)–(i), plant biomass = 2.29g; (j)–(l) plant biomass = 20.23g. Solid lines show regression lines for statistically significant relationships. Regression lines were calculated based on standardized major axis regression.

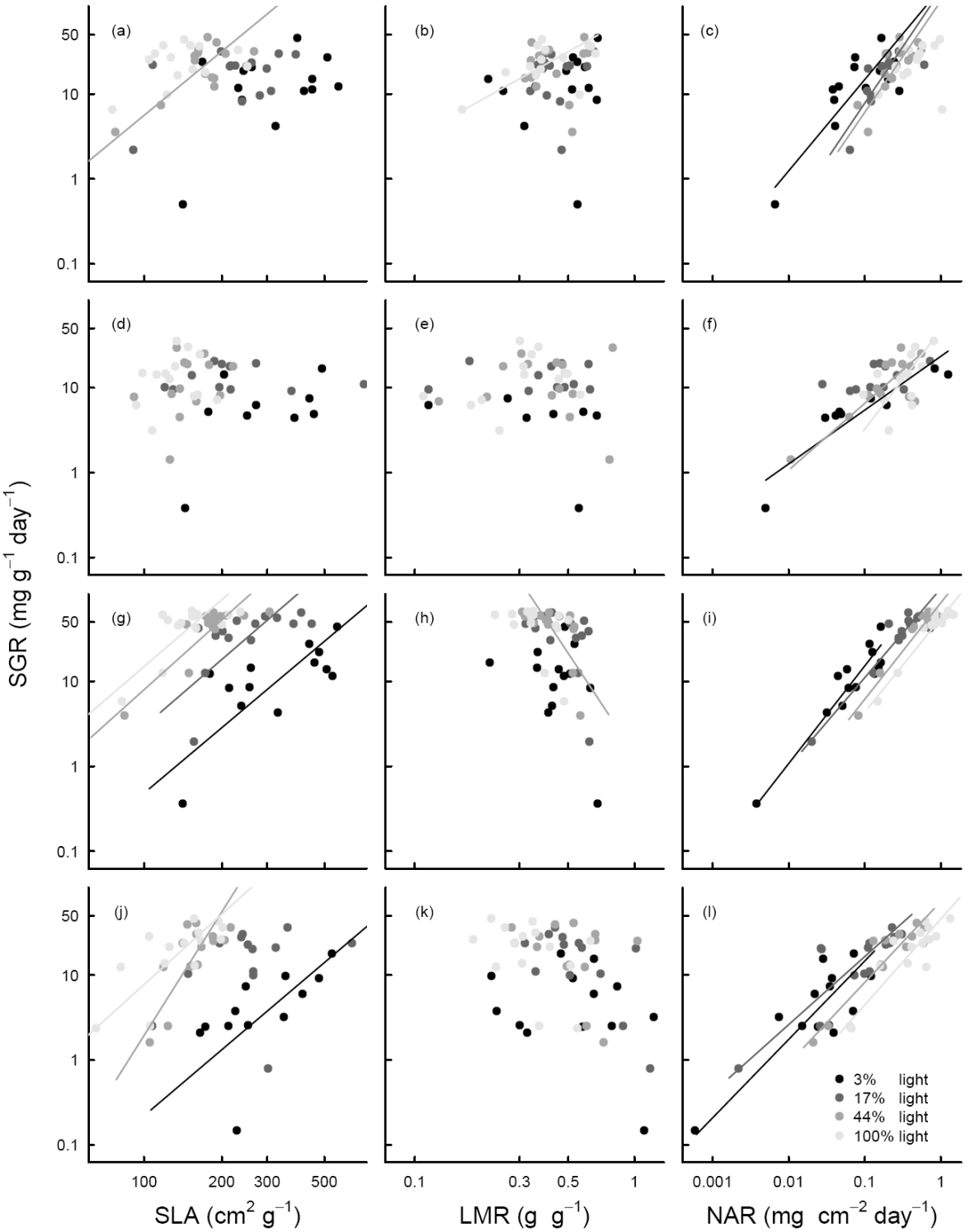
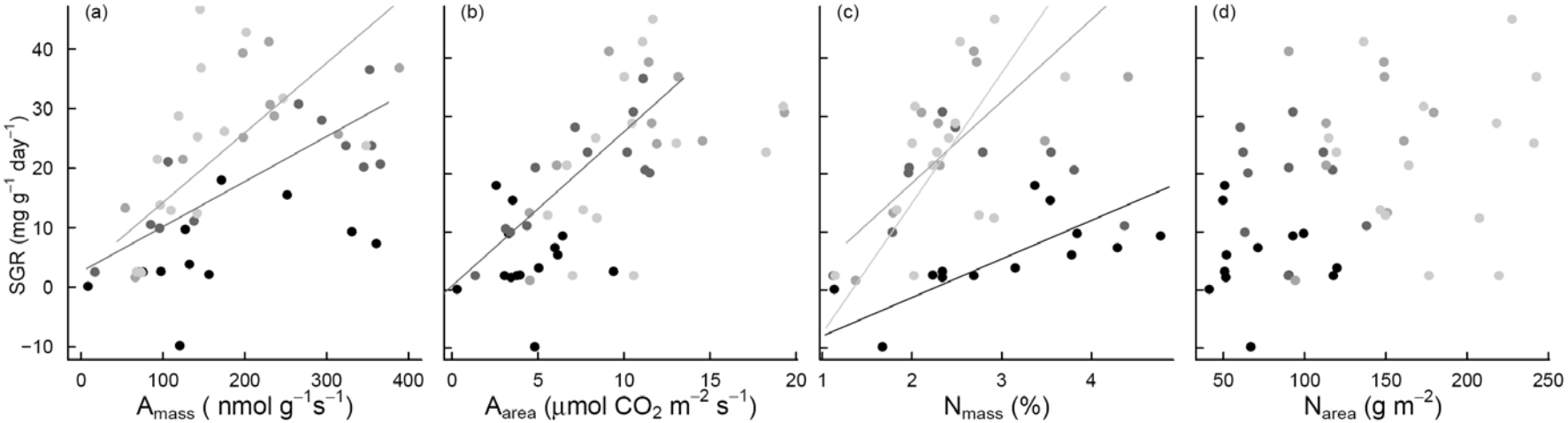


Fig. 8. Correlations between SGR and A_{mass}, A_{area}, N_{mass} and N_{area} at 3%, 17%, 44% and 100% of day light. Legend is the same as Fig. 7. Solid lines show regression lines for statistically significant relationships. Regression lines were calculated based on standardized major axis regression.



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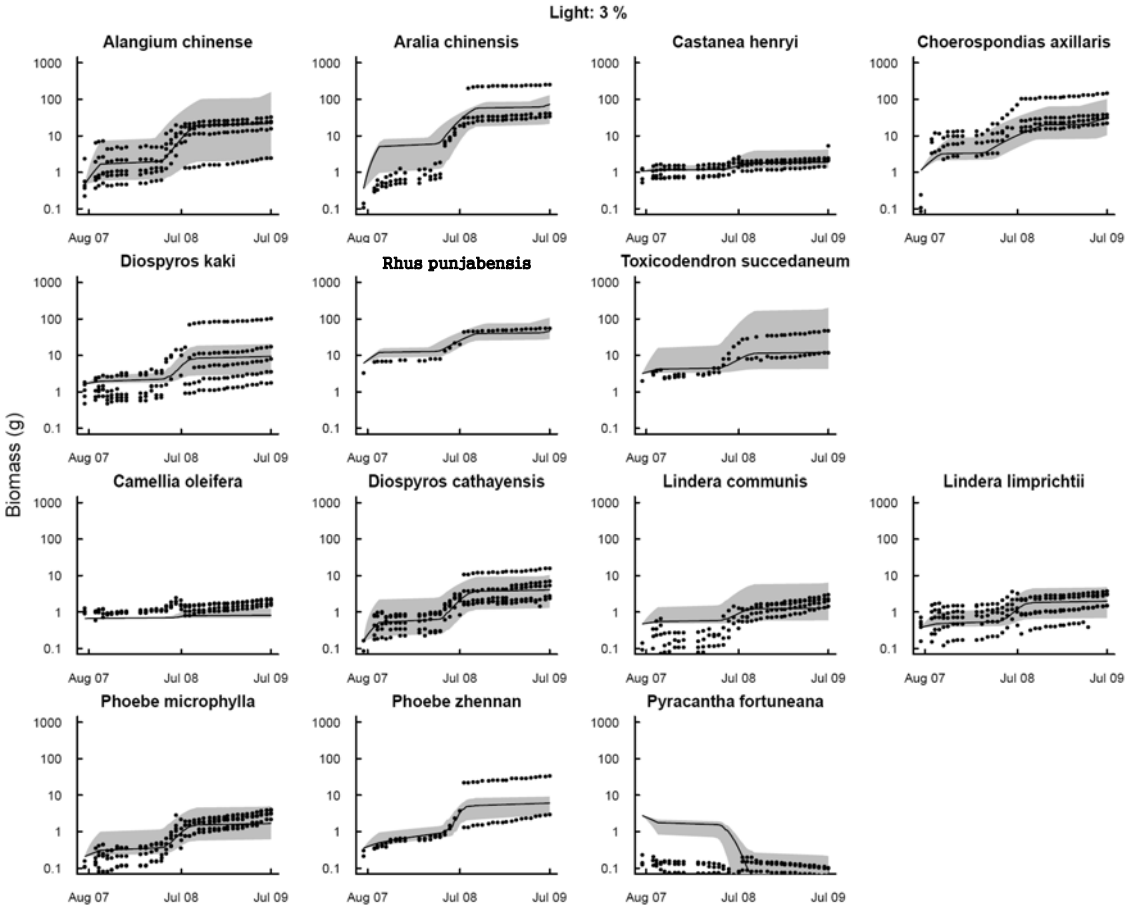
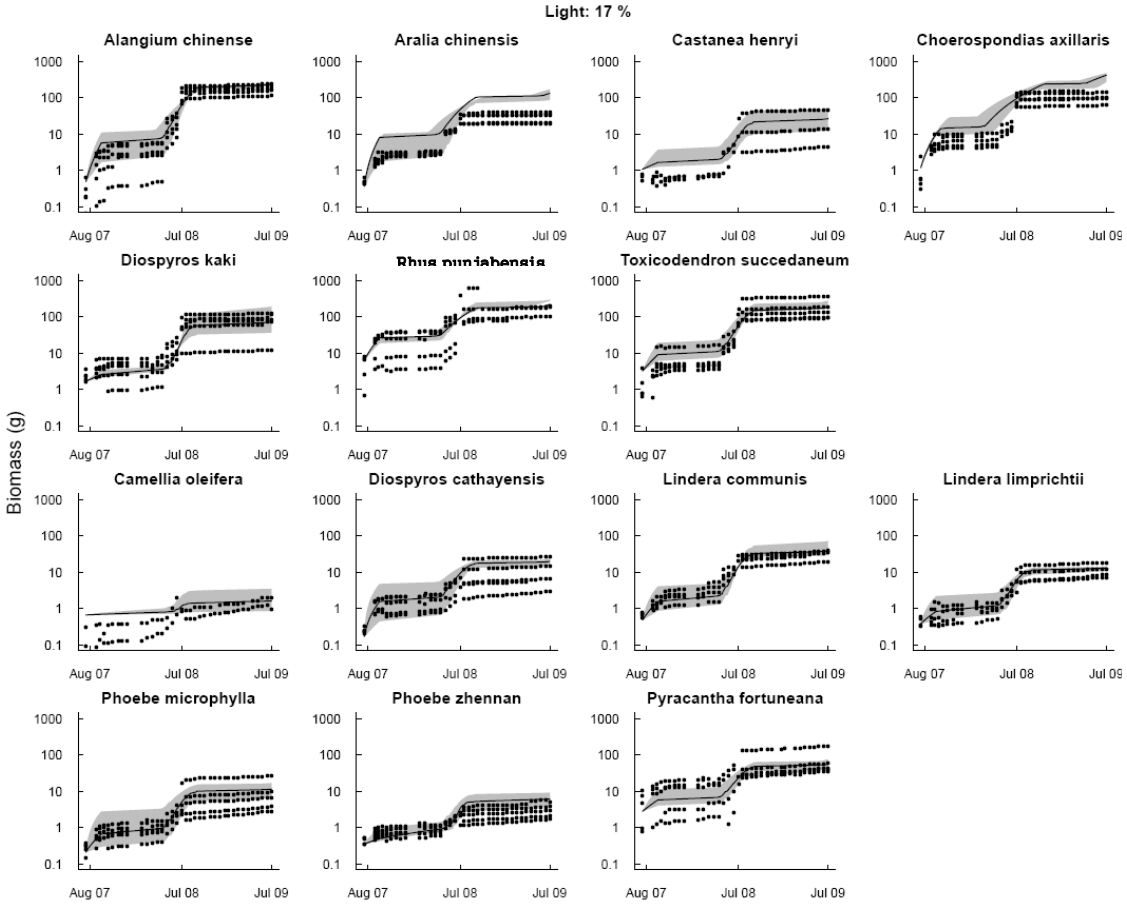
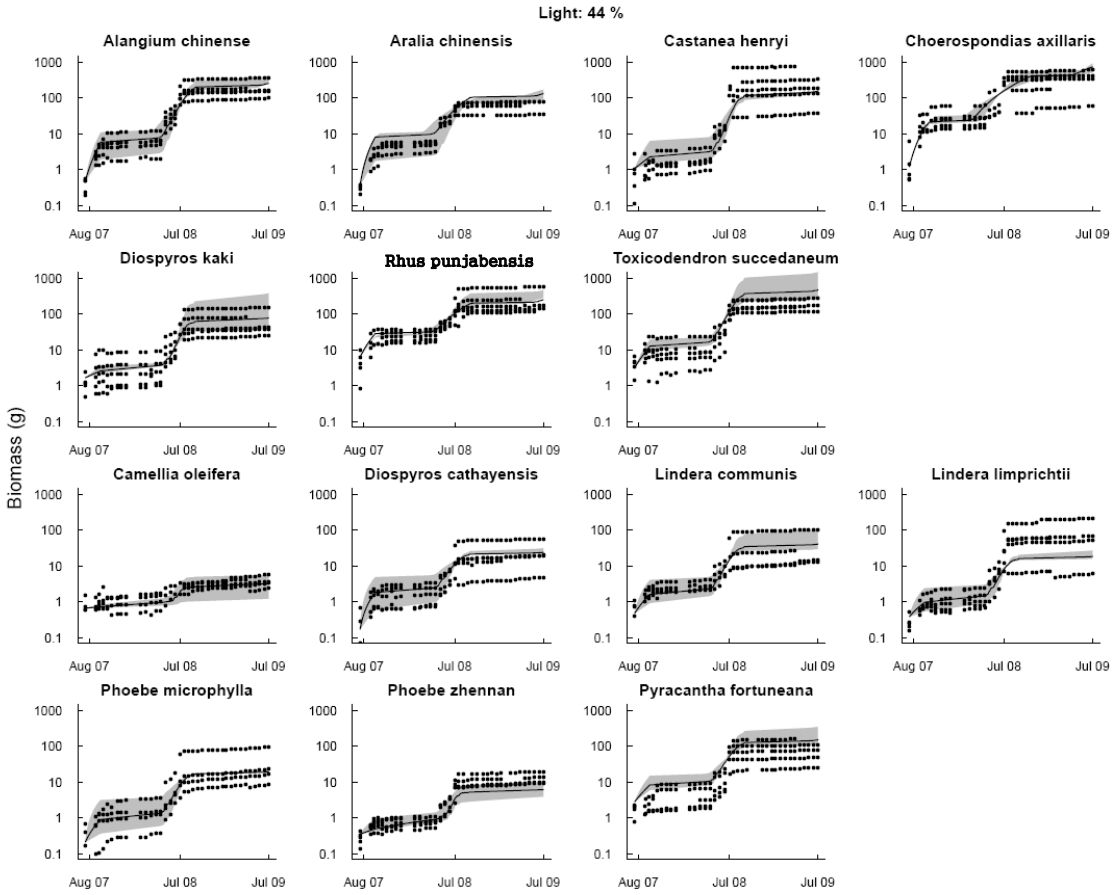
Appendix A: Model comparison. Akaike information criterion (AIC) and Bayesian information criterion (BIC) from different models (see Methods for explanation) were compared. Numbers in bold show the best choice of model under each category.

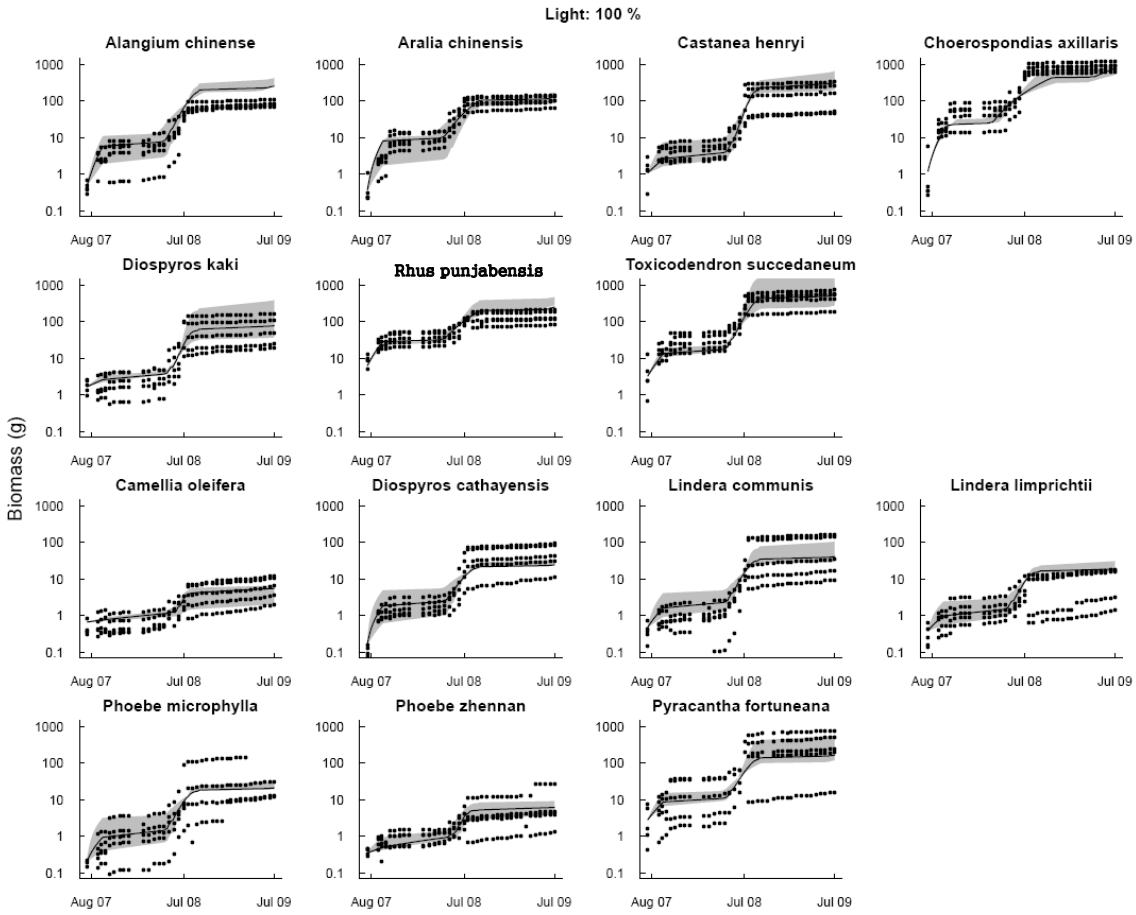
	AIC	*BIC*
All species-specific model	**27594**	**27866**
1-parameter global models		
β	24160	24399
T_{cp}	**23332**	**23571**
G0	23423	23662
$L_{0.5}$	24017	24256
L_{min}	24433	24672
T_{mid}	23758	23997
T_{sc}	23473	23712
2- parameter global models (all include T_{cp} as global)		
G0	**23357**	**23565**
T_{sc}	23595	23803
L_{min}	23931	24139
$L_{0.5}$	24101	24309
β	24301	24509
T_{mid}	45231	45438
3- parameter global models (all include T_{cp} and $G0$ as global)		
T_{sc}	**23207**	**23383**
T_{mid}	23556	23732
β	24238	24414
L_{min}	24327	24503
$L_{0.5}$	24722	24898
4- parameter global models (all include T_{cp}, $G0$ and T_{sc} a global)		
β	24127	24271
$L_{0.5}$	24392	24536
L_{min}	**23939**	**24083**
T_{mid}	24900	25044
All global model	**32375**	**32390**

Appendix B: Biomass prediction for each species under each light treatment (3%, 17%, 44% and 100%) from growth model (solid line) with 95% confidence interval (grey shading) against biomass accumulation from observation and estimation from simple stem volume–biomass allometric equations (dots).




Light: 17 %
Alangium chinense
Aralia chinensis
Castanea henryi
Choerospondias axillaris
Diospyros kaki
Rhus punjabensis
Toxicodendron succedaneum
Camellia oleifera
Diospyros cathayensis
Lindera communis
Lindera limprichtii
Phoebe microphylla
Phoebe zhennan
Pyracantha fortuneana
Biomass (g)
1000
100
10
1
0.1
Aug 07
Jul 08
Jul 09


Light: 44 %
Alangium chinense
Aralia chinensis
Castanea henryi
Choerospondias axillaris
Diospyros kaki
Rhus punjabensis
Toxicodendron succedaneum
Camellia oleifera
Diospyros cathayensis
Lindera communis
Lindera limprichtii
Phoebe microphylla
Phoebe zhennan
Pyracantha fortuneana
Biomass (g)
1000
100
10
1
0.1
Aug 07
Jul 08
Jul 09


Light: 100 %
Alangium chinense
Aralia chinensis
Castanea henryi
Choerospondias axillaris
Diospyros kaki
Rhus punjabensis
Toxicodendron succedaneum
Camellia oleifera
Diospyros cathayensis
Lindera communis
Lindera limprichtii
Phoebe microphylla
Phoebe zhennan
Pyracantha fortuneana
Biomass (g)
1000
100
10
1
0.1
Aug 07
Jul 08
Jul 09

Appendix C

Species mean value (±SD) of specific leaf area (SLA), leaf mass ratio (LMR) and net assimilation rate (NAR) under different light conditions and age. Values without SD indicate there was only one plant survived at the time of measurements.

	SLA (August 2008)				SLA (July 2009)			
	L	M	H	O	L	M	H	O
Alangium chinense	581±151	471±238	312±91	221±18	327±208	287±45	215±49	190±59
Aralia chinensis	504±152	344±147	187±32	144±57	493±6	178±97	130±34	143±23
Camellia oleifera	133±32	196±194	79±10	86±15	136±17	186	98	66±5
Castanea henryi	317±36	255±53	197±7	144±9	382±1	467±235	146±30	140±16
Choerospondias axillaris	568±109	332±68	213±41	188±38	424±100	73±23	210±69	172±26
Diospyros cathayensis	265±32	222±164	188±35	231±93	259±54	235±30	93±81	106±26
Diospyros kaki	440±62	245±33	158±6	126±22	213	197±127	157±20	119±30
Lindera communis	220±43	236±51	175±26	117±21	299±186	143±36	172±51	111±12
Lindera limprichtii	234±26	218±57	204±11	163±11	161	203±22	136±6	133±16
Phoebe microphylla	266±21	197±43	201±61	140±16	250±2	95	150±43	116±8
Phoebe zhennan	188±37	215±93	152±47	122±13	184	161±74	130±6	105±11
Pyracantha fortuneana	180±21	229±62	195±105	106±4	142	397±276	128±27	113±50
Rhus punjabensis	592±248	299±75	186±31	134±7	410±100	210±42	181±74	137±37
Toxicodendron succedaneum	571±180	380±87	170±14	127±14	500	287±45	155±15	156±63

	LMR (August 2008)				LMR (July 2009)			
	L	M	H	O	L	M	H	O
Alangium chinense	0.56±0.15	0.42±0.05	0.38±0.06	0.4±0.07	0.32±0.33	0.46±0.04	0.33±0.15	0.35±0.06
Aralia chinensis	0.48±0.33	0.36±0.18	0.36±0.04	0.4±0.06	0.27±0.35	0.43±0.15	0.35±0.12	0.28±0.16
Camellia oleifera	0.54±0.04	0.5±0.14	0.51±0.11	0.4±0.24	0.61±0.1	0.37	0.64	0.45±0.03
Castanea henryi	0.28±0.08	0.42±0.08	0.35±0.02	0.39±0.08	0.28±0.06	0.54±0.21	0.56±0.31	0.28±0.11
Choerospondias axillaris	0.37±0.06	0.36±0.07	0.29±0.04	0.31±0.05	0.46±0.07	0.56±0.14	0.37±0.13	0.24±0.09
Diospyros cathayensis	0.5±0.02	0.36±0.02	0.32±0.08	0.38±0.07	0.27±0.17	0.54±0.24	0.47±0.33	0.23±0.15
Diospyros kaki	0.23±0.06	0.39±0.04	0.38±0.04	0.44±0.07	0.01	0.67±0.17	0.35±0.09	0.31±0.1
Lindera communis	0.63±0.08	0.63±0.03	0.59±0.06	0.63±0.07	0.41±0.21	0.65±0.08	0.42±0.36	0.5±0.04
Lindera limprichtii	0.59±0.07	0.51±0.06	0.6±0.08	0.55±0.14	0.54	0.52±0.07	0.52±0.04	0.31±0.26
Phoebe microphylla	0.61±0.08	0.61±0.03	0.61±0.03	0.6±0.02	0.4±0.38	0.47	0.58±0.18	0.39±0.05
Phoebe zhennan	0.49±0.09	0.48±0.09	0.5±0.04	0.52±0.1	0.06	0.48±0.22	0.58±0.27	0.32±0.1
Pyracantha fortuneana	0.47±0.12	0.37±0.17	0.36±0.07	0.39±0.06	0.68	0.35±0.19	0.52±0.21	0.36±0.16
Rhus punjabensis	0.29±0.06	0.43±0.09	0.37±0.11	0.36±0.05	0.38±0.2	0.39±0.39	0.49±0.04	0.51±0.11
Toxicodendron succedaneum	0.47±0.17	0.34±0.12	0.38±0.05	0.37±0.02	0.2	0.46±0.04	0.42±0.13	0.36±0.02

	NAR (August 2008)				NAR (July 2009)			
	L	M	H	O	L	M	H	O
Alangium chinense	0.075±0.002	0.186±0.075	0.282±0.047	0.393±0.059	0.926±0.916	0.153±0.024	0.332±0.117	0.379±0.136
Aralia chinensis	0.753±1.188	0.121±0.054	0.186±0.019	0.361±0.185	0.456±0.551	0.161±0.075	0.214±0.148	0.508±0.71
Camellia oleifera	0.008±0.003	0.055±0.066	0.118±0.077	1.218±2.256	0.005±0.001	0.264	0.049	0.092±0.016
Castanea henryi	0.052±0.017	0.23±0.084	0.536±0.062	0.896±0.305	0.039±0.012	0.05±0.029	0.517±0.311	1.028±0.579
Choerospondias axillaris	0.056±0.022	0.096±0.022	0.236±0.038	0.31±0.061	0.042±0.014	0.638±0.268	0.15±0.106	0.196±0.08
Diospyros cathayensis	0.148±0.026	0.541±0.607	0.271±0.098	0.265±0.032	0.142±0.086	0.163±0.066	0.814±1.179	0.47±0.456
Diospyros kaki	0.184±0.042	0.241±0.046	0.448±0.035	0.536±0.118	4.267	0.201±0.153	0.32±0.119	0.628±0.227
Lindera communis	0.057±0.025	0.24±0.063	0.428±0.242	0.505±0.147	0.058±0.027	0.085±0.033	0.522±0.43	0.29±0.107
Lindera limprichtii	0.104±0.038	0.25±0.147	0.239±0.137	0.769±1.12	0.169	0.108±0.045	0.066±0.017	0.475±0.463
Phoebe microphylla	0.105±0.068	0.219±0.165	0.264±0.084	0.548±0.209	0.094±0.073	0.305	0.149±0.111	0.319±0.118
Phoebe zhennan	0.269±0.089	0.129±0.071	0.087±0.018	0.205±0.152	0.252	0.477±0.683	0.019±0.012	0.155±0.121
Pyracantha fortuneana	-0.265±0.01	0.491±0.635	0.407±0.209	0.569±0.107	-0.108	0.172±0.19	0.281±0.123	0.56±0.535
Rhus punjabensis	0.165±0.173	0.144±0.053	0.246±0.101	0.34±0.026	0.095±0.056	1.584±2.599	0.12±0.045	0.135±0.055
Toxicodendron succedaneum	0.042±0.01	0.258±0.119	0.561±0.034	0.799±0.074	0.087	0.153±0.024	0.439±0.132	0.53±0.159

CHAPTER 2

Survival-growth trade-off among subtropical tree seedlings in contrasting light environments

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Abstract

We investigated the performance trade-off among seedlings from 14 woody species coexisting in a subtropical forest in southwest China. Seedlings were grown in shade houses and open quadrats representing a gradient of light conditions (3%, 17%, 44% and 100% of full day light). We documented seedling survival and biomass accumulation over two years from August 2007 to July 2009; then we estimated a size-corrected relative growth rate (SGR) over this period. To understand which functional traits were related to seedling survival in the shade, we also investigated a suite of morphological, physiological and biomass partitioning traits. We found large variation of survival in the shade (3% of day light) among species and a trade-off between high-light growth rate and low-light survival in the first year. In the second year all of the species obtained high survival thus no trade-off was observed. Survival was explained by none of the examined traits, except that net assimilation rate (NAR) was positively related to seedling survival in evergreen species.

Introduction

Growth and survival are the two vital performance for any living organism (Hunt, 1982). As for a species, growth and survival determine the spatial and temporal patterns in its distribution. As for a forest community, species' responsiveness of growth and survival to fluctuations and disturbance have strong influences on the modification in forest composition during succession (Clark & Clark, 1992, Kobe & Coates, 1997, Pacala, Canham, Saponara *et al.*, 1996).

The performance trade-off is widely accepted in community ecology. One point of view assumes a better performance (growth or survival) under one set of conditions will reduce the performance under another set of conditions. For example, if a species has higher growth rate than another species in deep shade, it should have lower growth rate than the other in forest gaps (Givnish, 1988, Latham, 1992, Pacala, Canham, Silander et al., 1994, Sack & Grubb, 2001). On the contrary, the trade-off between survival in low-resource condition and growth in high-resource condition has also been proposed in diverse forest seedlings (Kitajima, 1994, Kobe, Pacala, Silander et al., 1995, Lin, Harcombe, Fulton et al., 2002), where light is the main resource affecting leaf traits, regulating plant growth and survival, and determining the distribution of plants. Theoretically, species coexistence in a community requires each species to outperform other species under a certain situation (Macarthur & Levins, 1964). This imply a rank reversal in performance between two situations.

The first view suggests survival is determined by species with low light carbon acquisition capacities, i.e. low-light survival is realized through enhanced low-light growth. The enhanced growth could help plants to escape the risk of being small and improve the overall energy status for resistance against pathogen, herbivory damage but at the expense of allocation to storage (Chapin, Schulze & Mooney, 1990, Kobe *et al.*, 1997). Other researchers found the evidence is mixed. For example, Walters & Reich (1996) found low-light survival was related to low-light growth, Kitajima (1994) and Veenendaal (1996) found low-light survival was negatively related to low- or high-light growth. There were other people found low-light RGR despite of the large variation in shade tolerance of seedlings (Grubb, 1996, Bauer, 1945). These researches suggested conservation of carbon may be realized by reducing dark respiration instead of carbon gain (Reich 2003). It was also suggested slow growing

species have low demands and are therefore less likely to exhaust limiting resources (Grime&Hunt 1975, Chapin 1980).

There is still argument about the mechanisms due to different aspects from different authors and a functional understanding of seedling mortality in the shade can improve our knowledge about it.Therefore we investigated the survival of seedlings in 14 subtropical woody plant species along an experimental irradiance gradient over two years. We measured a suite of morphological, physiological, biomass partitioning traits aiming to find out the if any of these trait lead to seedling mortality. We also tested two kinds of performance trade-offs which may promote species coexistence: (a) a low-light survivorship vs high light growth rate trade-off between species and (b) a low-light growth rate vs high-light growth rate trade-off.

Materials and Methods

Study site and experimental design

Details of the experimental design and treatment of seedlings were described in Chapter 1 and only a brief account of the essentials is given here. This study was conducted from August 2007 to July 2009 in an experimental garden near Dujiangyan, southwest China (31˚04’ N, 103˚43’ E). The 14 species used in this study are all woody species commonly found in the subtropical forest in that region. There were 7 species from broadleaved-evergreen and 7 from broadleaved-deciduous groups. The broadleaved-evergreen species were *Camellia oleifera* (Co, Theaceae), *Diospyros cathayensis* (Dc, Ebenaceae), *Lindera communis* (Lc, Lauraceae), *Lindera limprichtii* (Ll,Lauraceae), *Phoebe microphylla* (Pm, Lauraceae), *Phoebe zhennan* (Pz, Lauraceae), *Pyracantha fortuneana* (Pf, Rosaceae). The broadleaved-deciduous were *Alangium chinense* (Alc, Alangiaceae), *Aralia chinensis* (Arc, Araliaceae), *Castanea henryi* (Ch, Fagaceae), *Choerospondias axillaris* (Ca, Anacardiaceae), *Diospyros kaki* var. *silvestris* (Dk, Ebenaceae), *Rhus punjabensis* (Rp, Anacardiaceae) and *Toxicodendron succedaneum* (Ts, Anacardiaceae). Nomenclature followed “Flora of China” (ECCAS, 1974–1999).

We set up five shade houses for each of the three shade levels (3, 17, 44% of daylight) and five open quadrates representing conditions with 100% light availability. Seeds of the 14 species were collected and germinated in March 2007 under a shade

cloth in a nursery near Dujiangyan. Four seedlings of each species were transplanted into each shade house and open quadrate in August 2007, yielding a total of 1120 pots with a single test plant each. The pots were arranged in a hexagonal pattern with a distance of 0.5 m between neighboring pots (0.8 m between the centers of neighboring pots) to avoid shading. Two weeks after moving pots to shade houses, we replaced dead seedlings with ones of the same species sown at the same time. Plants were watered every 3–4 days or when the soil was dry.

Survival censorship and growth of seedlings

This experiment started on 16 August 2007 thus it was referred to day 1. We then examined seedling survival on day 40, 70, 100, 206, 231, 296 and 350 during the first year, as well as at the end of the experiment in July 2009 for the second year. For the first year, dead seedlings were noted and replaced by extra seedlings from the same species growing in the nursery, which were sown at the same time as seedlings in the shade houses. The replacement of the dead seedlings was done to ensure enough replicates for growth analysis. The death of these extra seedlings was not included in the survival survey so that we could compare seedling survival based on a same total number. For the second year, dead seedlings were noted and no seedling replacement was done.

We measured the height and stem diameter of each existing seedling every second week from the start of the experiment in August 2007 to July 2009. Growth rates of each species under 3% and 100% light condition were calculated based on a common seedling biomass of 1.5g and 17g, respectively, because they were the average seedling biomass under each light condition. We used a mechanistic model based on power-law function with temperature variation and light availability integrated as shown in Chapter 1.

Functional traits

We measured or calculated the following traits before the harvest of each plants: specific leaf area (SLA, $cm^2\ g^{-1}$), leaf mass ratio (LMR, %), stem mass ratio (SMR, %), root mass ratio (RMR, %), net assimilation rate (NAR, mg $cm^{-2}\ day^{-1}$), leaf thickness (T, mm), total nitrogen content (N_{mass}, % dry mass), stomatal conductance (gs_{area}, μmol $H_2O\ m^{-2}\ s^{-1}$), photosynthetic capacity (A_{max}, μmol $CO_2\ m^{-2}\ s^{-1}$) and

photosynthetic nitrogen-use efficiency (PNUE, μmol g^{-1} s^{-1}). The details of measurements was described in Chapter 1.

Results

Seedling survival rate along time

Seedling survival of *Castanea henryi* dropped dramatically around day 99, while other species had gradual loss of seedlings (Fig. 1).

The seedling survival responses to light varied among species, between leaf habits and seedling age. No species had a higher survival or growth in shade than in sun as described for some dipterocarp seedlings. Evergreen species generally had better survivorship (survival rate $\geqslant$ 0.75) than deciduous species under low irradiance, whereas under higher irradiance the survival rate were similar between these two groups (Table 1). Within each leaf habit group, early successional species generally had lower survival rate than intermediate and late successional species at low light (except for Alc and Lc). In the first year, seedlings either survived better in higher than lower irradiance, or had similar survival rate along light gradient (Table 1). In the second year, all species had high survival rate ($\geqslant$0.8) at any light level.

According to the seedling mortality under low light in the first year as shown in Table 1, species rank in shade tolerance was: *Diospyros cathayensis* (E) = *Lindera limprichtii* (E) > *Lindera communis* (E) = *Phoebe microphylla* (E) > *Alangium chinense* (D) = *Choerospondias axillaris* (D) = *Diospyros kaki* (D) > *Camellia oleifera* (E) = *Phoebe zhenan* (E) > *Aralia chinensis* (D) = *Pyracantha fortuneana* (E) > *Toxicodendron succedaneum* (D) > *Rhus punjabensis* (D)> *Castanea henryi* (D), where E and D indicate evergreen and deciduous species. Evergreen species generally had higher shade tolerance than deciduous species, possibly because of their thick leaves (Walters & Reich, 1999).

Survival rate and traits

Under 3% light, survival rate was negatively related to A_{area} ($p=0.004$, $r^2=0.5$), A_{mass} ($p=0.01$, $r^2=0.42$) and PNUE ($p=0.01$, $r^2=0.43$). Evergreen species, NAR was positively related to survival rate under 3% light in evergreen species ($p<0.001$,

r^2=0.96) (Fig. 3). There was no relationships between survival rate under 3% light and other functional traits.

Survival – growth trade off

Low- and high-light SGR was neither positively nor negatively correlated when all of the species were taken into account or tested within leaf habit groups (Fig. 2a). except for Pf, evergreen and deciduous species were segregated on the plot with deciduous species occupied the upper-right region (high SGR in both light) and evergreen species the lower-left region (low SGR in both light). Within deciduous species, Ch had the lowest SGR under 3% light and the highest under 100% light, whereas Arc had the highest SGR under 3% light and the lowest under 100% light . The other species were placed between these two ends. Evergreen species exhibited relatively similar low-light growth rate except for Pf.

When all species were pooled no relation between survival and growth under low light, while among evergreen species there was positive relationship (r=0.78, p=0.039), indicating those grew faster in low light also survived better than those grew slower (Fig. 2b). Across all of the species, there was a trade-off between high-light growth and low-light survival rate (r=-0.56, p=0.039) (Fig. 2c), which indicated the trade-off between survival in the shade and growth potential in the light as suggested by previous researchers (e.g. Kitajima 1994, Pacala 1994).

Discussion

RGR rank reversal

Rank reversals in RGR over light gradients have been proposed as one of the mechanisms of niche differentiation and species coexistence (Givnish, 1988, Latham, 1992, Pacala *et al.*, 1994, Sack *et al.*, 2001). Several theoretical models predicted certain species will dominate at a given point along an environmental gradient due to their difference in the relative competence along this gradient (Grime 1977, 1979), while other researchers suggested rank retentions of RGR among species between contrasting environments (Kitajima, 1994, Poorter, 1999, Veneklaas & Poorter, 1998).

We failed to detect neither negative nor positive relationship between RGR in high and low light (Fig. 2), which reflected the rank retentions or rank reversals observed among the 14 species were not more than expected by random as also found previously (Kitajima 2003). Nonetheless, there were many crossovers among the RGR reaction norm to light of different species (Fig. 1 in Chapter 1) indicating the relative competence somehow varied between species along light gradient at least for certain species-pairs. The extreme cases was observed in the light demanding species Pf and Ch. At a plant biomass of 20.23g, Pf and Ch had the lowest RGR in 3% light and highest RGR in 100% light among species of their own groups (evergreen for Pf, deciduous for Ch). It showed light-demanding species indeed had superior performance than other species in the light. However in our study, there was large overlap in shade tolerance among species (Table 1). The large species number and small difference in species shade tolerance may explain the failure in detecting RGR rank reversal in our study.

Armed with modelling approach, we predicted the growth of plants under a certain light condition from 0% to 100%, and at different seedling biomass. Our result raised several points concerning seedling growth rank reveral. First, rank reversals can only be observed when low light is low enough. We found no significant negative correlations in RGR rank between low and high light once the low light is set above 2% of full light (data not shown). Previous studies found consistent ranking in growth between species often had moderately low light, but not extremely low light treatment, e.g. 2% in Kitajima (1994) and 3% of full light in Poorter (1999) study and 3 %. Second, rank reversals can be masked in plants' early ontogeny, or small size. Small-seeded, shade-intolerant plants may benefit from initial burst of RGR due to their very high specific leaf area, so that they have high growth rate both in light and shade (Grubb, 1998, Maranon et al., 1993, Grubb et al., 1996). This advantage will gradually diminish as plants grow larger and large-seeded, shade-tolerant species will finally take over shade-intolerant species in the shade (Grubb et al., 1996). Third, comparing species from the same leaf habit group may uncover the underlying mechanisms. There are remarkable distinction in leaf morphology and whole-plant carbon balance strategy between deciduous and evergreen species (Walters et al., 1999). Photosynthesis, nitrogen, morphology are different (Fig. 5).

Age-/size-dependent trade-off

Under 3% of light, these species encompassed a wide and continuous range in their survival (Table 1). At one extreme of these species is *Castanea henryi,* a light-demanding deciduous species which experienced 80% seedling death in low light treatment while all seedlings of this species survived in the open quadrates, and has the highest relative growth rate under 100% light when compared with other species at a common biomass of 20.23g (Fig. 1 in Chapter 1). At the other extreme are species, such as evergreen species *Diospyros cathayensis* and *Lindera limprichtii*, whose seedlings survive equally well in shade and sun, but have limited growth in sun (Fig. 1 in Chapter 1)

Our results showed evidence for a trade-off between survival in low light condition and RGR in high light condition as suggested as species coexistence by previous studies (Kitajima, 1994, Kobe, Pacala, Silander et al., 1995, Lin, Harcombe, Fulton et al., 2002). However, this trade-off was age-dependent: it was only observed in first-year seedlings. Low-light survival in second-year seedlings was not different among species. The age-dependent survival has been observed before (Perez-Ramos, Gomez-Aparicio, Villar et al., 2010).

Conclusions

Survival and growth of seedling have large influences on forest dynamics. The trade-offs between these two fitness components and between micro-climate have been proposed to be important mechanisms for species coexistence in a forest community. Understanding how survival and growth related in varying light conditions and how functional traits determine the processes is of paramount significance to understand interspecific differences contribute to community structure. We did not find either rank reversal or rank retention in species growth rate between high and low light, but there were substantial crossovers between growth norms in response to a light gradient from 3% to 100%. In low light, high seedling survival was guaranteed by high growth rate in evergreen species while in deciduous species such case was not found. The trade-off between growth rate in light and survival in shade was again proved in our study. It reflects species are place along a strategy spectrum which run from high growth in light, low survival in shade to remaining grow slowly in light with high survival in shade. However, this trade-off is age- or size-dependent.

Tables

Table 1. Seedling survival rate at the end of the first year along a light gradient (3%, 17%, 44% and 100% of day light)

	Lear habit	Successional stage	First year survival rate			
			3%	17%	44%	100%
Alangium chinense	Deciduous	Early	0.90	1.00	0.85	0.95
Aralia chinensis	Deciduous	Intermediate	0.75	1.00	0.95	1.00
Castanea henryi	Deciduous	Early	0.20	0.70	0.85	1.00
Choerospondias axillaris	Deciduous	Intermediate	0.85	1.00	1.00	1.00
Diospyros kaki	Deciduous	Intermediate	0.90	0.95	0.95	1.00
Rhus punjabensis	Deciduous	Early	0.30	1.00	0.95	0.90
Toxicodendron succedaneum	Deciduous	Intermediate	0.65	1.00	1.00	1.00
Camellia oleifera	Evergreen	Intermediate	0.85	0.75	0.90	1.00
Diospyros cathayensis	Evergreen	Intermediate	1.00	1.00	1.00	1.00
Lindera communis	Evergreen	Early	0.90	0.95	1.00	1.00
Lindera limprichtii	Evergreen	Intermediate	1.00	0.80	1.00	0.95
Phoebe microphylla	Evergreen	Intermediate	0.95	1.00	0.95	1.00
Phoebe zhennan	Evergreen	Late	0.85	0.95	1.00	1.00
Pyracantha fortuneana	Evergreen	Early	0.75	1.00	1.00	1.00

Figures

Fig. 1. Percentage of seedling survival of each species under 3% light in the first year. Points were slightly jittered to avoid overlapping.

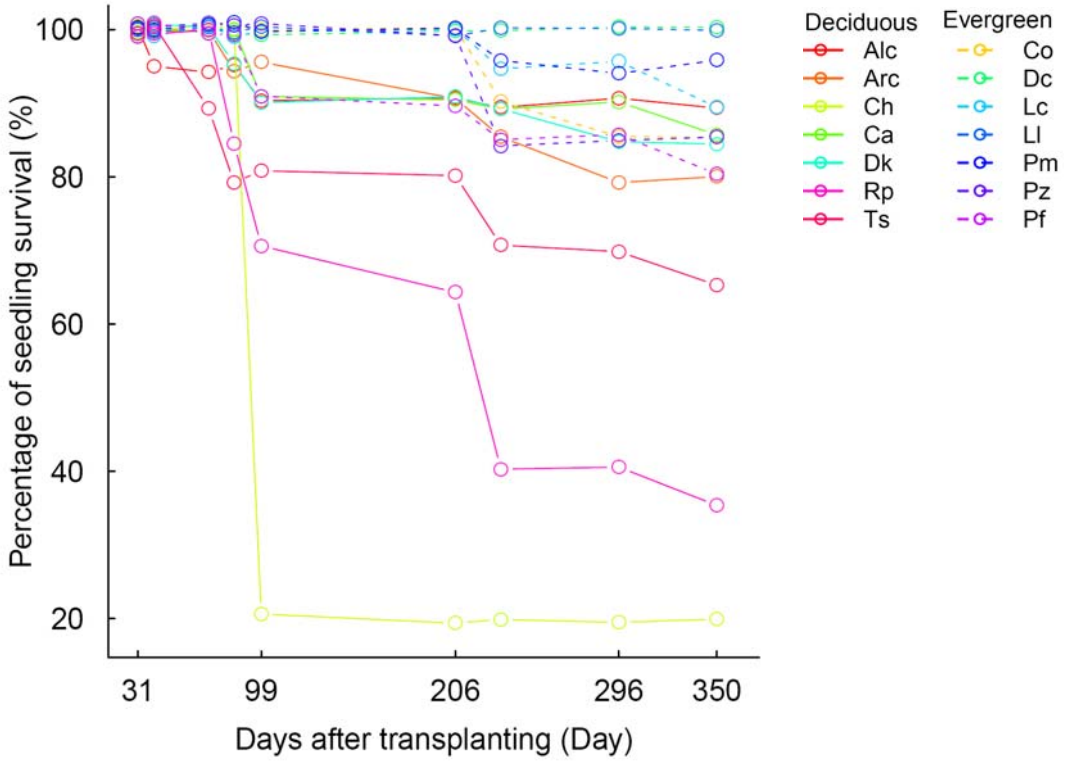


Fig. 2. Performance trade-off between RGR at 3% light, RGR at 100% light and survival rate at 3% light. RGR at 3% and 100% light was estimated at a common plant biomass of 1.5g and 17g, respectively. These biomass value were chosen based on the median plant biomass at harvest under each light condition. Grey points indicated evergreen species and circles indicated deciduous species.

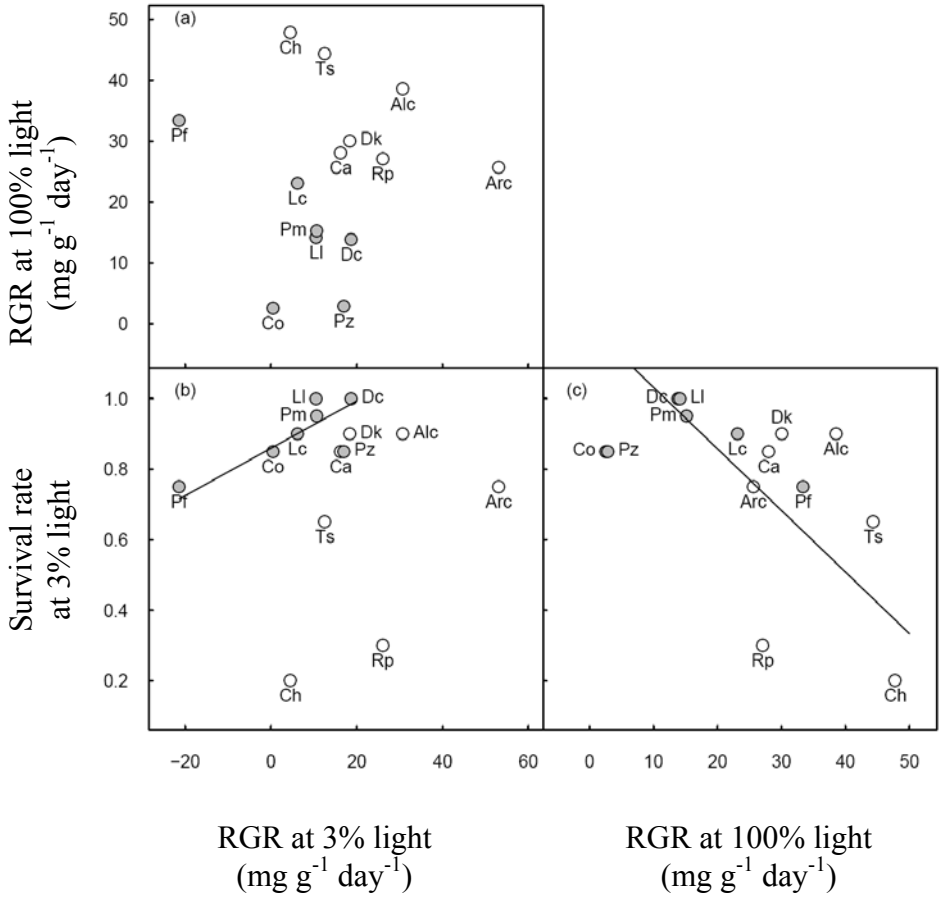
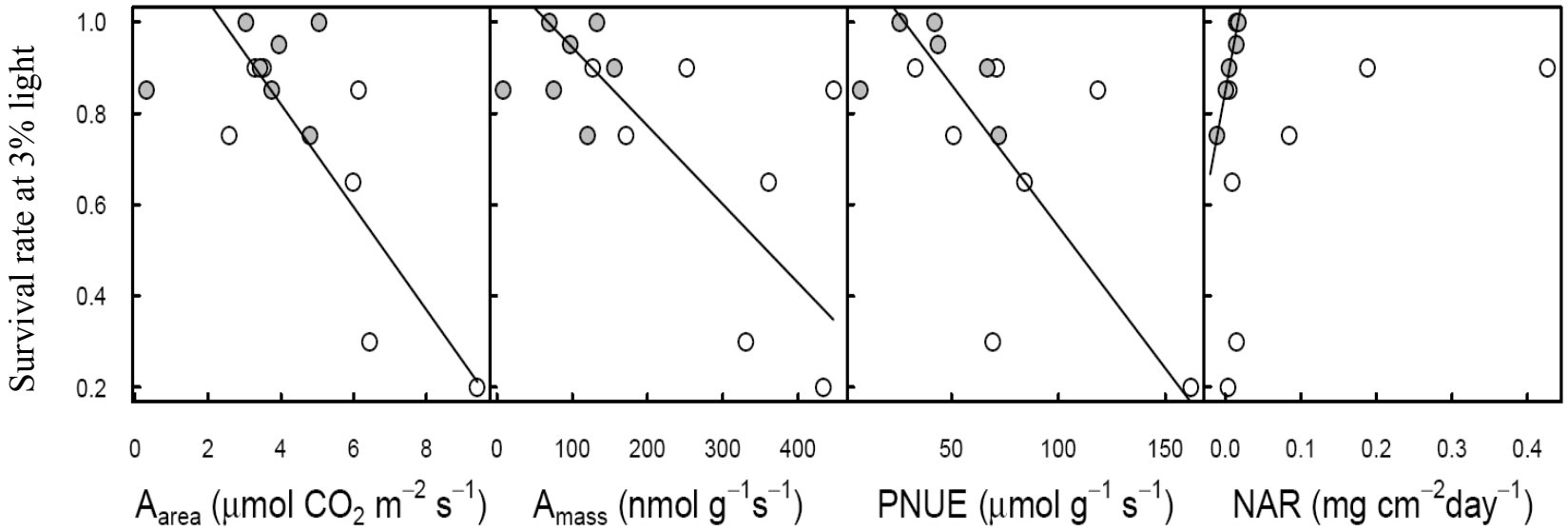


Fig. 3. Survival rate at 3% light in relation to physiological traits. A_{area} = Photosynthetic capacity on a area basis. A_{mass}= Photosynthetic capacity on a mass basis. PNUE= photosynthetic nitrogen-use efficiency. NAR=net assimilation rate. Grey points indicated evergreen species and circles indicated deciduous species. Solide lines showed the regression lines of significant correlations between survival at 3% light and traits.



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CHAPTER 3

Seedling survival, growth and functional traits in a Chinese subtropical forest along a light gradiant

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Abstract

The seedling stage of subtropical shrubs and trees is very likely more vulnerable to disturbance and environmental conditions than the seed or adult tree stage. It is thus particularly important to study the survival and growth of seedlings in the forest understory to predict species composition in the longer term. Here we present a two-year field experiment in which we transplanted seedlings of 14 woody species representing three contrasting functional types along a light gradient into the understory of a subtropical forest in southwestern China. We assessed mortality and measured the growth rate of all transplanted individuals at intervals. To further understand the mechanisms leading to seedling mortality and growth, we examined three functional traits of transplanted individuals. We found that light availability was not the single critical factor determining seedling performance. Rather, seasonal competition and functional traits which enhanced a seedlings' resistance to multi-level stresses in the understory appeared to be of even greater importance at least during the initial establishment phase. However, our study does suggest that after this initial phase, light-demanding and shade-tolerant strategies are deployed by different species and that this niche differentiation may increase species coexistence in a heterogeneous habitat, where the former grow relatively faster in patches with better light conditions and the latter grow faster in patches with lower light.

Introduction

Studying seedlings of woody plants in their natural habitat is important because of the high mortality often incurred during this stage of the life cycle (Harper, 1977, Silvertown & Charlesworth, 2001). Woody seedlings usually grow in forest understory for many years before they reach the canopy. Light is a critical resource for seedlings to survive and grow, as the light condition in tropical forests is on the order of 0.5–2% of above-canopy light (Chazdon, 1988, Clark, Clark, Rich et al., 1996). Due to the magnitude of light heterogeneity observed in natural forest, it is usually assumed coexisting species fall along a shade tolerant–light demanding spectrum. Both shade-house experiments and field studies have shown that species differ in their shade tolerance (Kitajima, 1994, Poorter, 1999). It has been suggested that in low light, shade-tolerant species can enhance light-harvesting efficiency to maintain positive carbon gain. Shade-tolerant species typically have large specific leaf area (SLA) and a foliar display that maximizes light interception (Givnish, 1988). These morphological adjustments allow shade-tolerant species to use light efficiently, increasing growth rate and reducing mortality in the shade. However, some studies did not find these adjustments and questioned their general validity (Kitajima, 1994, Poorter, 1999, Walters & Reich, 2000).

Several reasons could explain deviations from the predicted pattern of high SLA and extensive foliar display in shade-tolerant species. First, in previous experimental studies, seedlings were protected from stressors such as herbivores, pathogens and temperature extremes that would normally occur under natural conditions in the field. Findings from such studies assume that seedling mortality is mainly caused by the collapse of the whole-plant carbon balance under low light. However, under field conditions, seedlings may be killed directly by other stressors, so seedlings should invest resources in defense and storage and not only in maximizing light interception. Second, previous field studies often lacked an experimental approach; that is, they were based on comparative observational approaches using seedlings already growing in the forest of unknown age. Furthermore, seedling occurrence could be affected by a number of uncontrolled, confounding environmental factors. Seedling age can be an important factor influencing seedling performance (Lusk & Warton, 2007, Niinemets, 2006). Third,

previous experimental studies on shade tolerance have mostly been conducted with first-year seedlings (Niinemets, 2006, Walters & Reich, 1999), whereas seedlings of non-pioneer species usually spend more than one year in the shaded forest understory before they grow out of it. Fourth, previous studies mostly focused on broad-leaved evergreen species from moist and wet tropical forests (Delissio, Primack, Hall *et al.*, 2002) or on deciduous species from temperate and boreal forests, whereas only few studies included both evergreen and deciduous species. The two plant functional types may use contrasting strategies to cope with shade, for example, shade-tolerant evergreen species minimize biomass loss through long leaf life span whereas shade-tolerant deciduous species accomplish low biomass turnover by low leaf mass ratio and not low leaf turnover rate (Walters *et al.*, 1999)

Here we present results from a two-year field experiment in which we transplanted seedlings of 14 woody species representing three contrasting functional types (broad-leaved evergreen, deciduous and coniferous species) along a light gradient into the understory of a subtropical forest in southwestern China. We assessed mortality and measured the growth rate of all transplanted individuals at intervals. To further understand the mechanisms leading to seedling mortality and growth, we examined three functional traits of transplanted individuals. Besides SLA, which reflects the potential for light interception, we also measured leaf mass ratio (LMR), which reflects whole-plant biomass partitioning, and wood density (WD), which reflects a wood property, to examine their influences on seedling mortality and growth. LMR is also related to plant shade adaptation as large allocation of biomass to leaves can increase the overall light interception of seedlings (Poorter, 2001). Finally, WD is an important indicator of successional status. In general, rapidly growing pioneer species have lower WD than late successional species (Augspurger, 1984a). Mortality rate has been found to be negatively related to WD for seedlings growing under controlled conditions (Kitajima, 1994) as low wood density makes stems less resistant to breakage and to fungal and pathogen attack (Augspurger, 1984b).

We answer the following questions. First, how are seedling survival and growth affected by light, species functional type, species identity, seedling age, growing season and soil conditions? Second, is there a trade-off between seedling survival and growth? Third, can interspecific variation in SLA, WD and LMR explain variation in seedling performance in the forest understory?

Materials and Methods

Study site and experimental design

The study was carried out from August 2007 to July 2009 at two forest sites near Dujiangyan, Sichuan, SW China. The prevailing vegetation type is secondary, mixed coniferous and broad-leaved subtropical forest. The climatic conditions are subtropical with a dry winter (November–April) and a warm and rainy summer (May–October). The annual average temperature is 15.2 °C and July average temperature is 25 °C. The mean annual precipitation is 1341 mm and the annual average relative humidity is above 80 % (Chen, 2000).

The 14 species studied are commonly found in subtropical forest in Dujiangyan. We included 6 evergreen broad-leaved, 6 deciduous broad-leaved and 2 evergreen coniferous species representing 9 families (Table 1). Seedlings of each species were sown in spring 2007 in a nursery near the field sites. We set up 6 quadrats at each of the two sites along a light gradient. Quadrats 1, 4, 7, 9 and 11 were in low light, quadrats 2, 5, 8 and 12 in high light and quadrats 3, 6 and 10 were in the open (simulating a forest gap). In August 2007, we transplanted four seedlings of each species into each of the 12 quadrats in a random pattern. A field map was drawn for each quadrat to help locating each seedling in the following surveys. We then checked the survival of seedlings two weeks after transplanting and found that all seedlings survived. We revisited each quadrat in March 2008, August 2008, January 2009 and July 2009, documented seedling survival, height and stem diameter (at 2 cm above ground) for all seedlings which were still alive. Live seedlings with broken stems were recorded as “broken”. Seedlings that could not be found were recorded as “missing”. Because most of the seedlings in quadrats 3 and 6 died because of human or cattle disturbance, data from these two quadrats were not included in analyses.

Characterization of abiotic factors

Light (light availability and quality) and soil factors (water and nutrient content, pH) were quantified in each quadrat. A list of the eight abiotic factors measured is given in Table 2.

Light availability was estimated by means of hemispherical canopy photography. Twenty photographs were taken at the seedling level within each quadrat using a horizontally leveled digital camera with a fish-eye lens and 180° field of view. Photographs were taken at evenly distributed locations within the range of seedling transplanting. Photographs were taken when the sun was blocked by clouds, ensuring homogeneous conditions of illumination at the understory and a correct contrast between canopy and sky. We used Hemisfer 1.5.0 (WSL Birmensdorf, Switzerland) to analyze the pictures and calculated average leaf area index (LAI) for each quadrat using the LiCor LAI 2000 method with correction (Schleppi, Conedera, Sedivy *et al.*, 2007). We measured the ratio of red to far-red photon flux density (R:FR, R, 655–665 nm; FR, 725–735 nm) as an indicator of light quality above each seedling using an SKR 660/730 (Red /Far Red) Measuring System (Skye Instruments Ltd, UK). The decrease in R:FR is the result of an increase in FR irradiance caused by reflection of the FR portion of sunlight by the foliage of neighboring plants (Aphalo, Ballare & Scopel, 1999). Many plants are sensitive to changes in R:FR which can be considered as a signal of shading and proximity to other plants (Aphalo & Lehto, 2001). We also measured photosynthetically active radiation (PAR) at the same location using SKP 215 PAR Quantum sensor (Skye Instruments ltd, UK) as a complementary means of evaluating field light condition.

In March 2008, we sampled the upper 10 cm of the soil using an auger (3 cm in diameter) at 4 points in each quadrat, and mixed them to produce one composite sample per quadrat. Soil samples were oven-dried, ground and analyzed for standard chemical properties (FOSS 2200, Foss Tecator AB, Sweden). Three soil properties were determined: acidity (with a pH meter), total nitrogen (using a Kjeldahl digestion and distillation-titration of the produced ammonium) and total phosphorus. Soil water content was obtained as follows: soil water content = (soil fresh weight – soil dry weight)/ soil fresh weight.

Seedling growth and morphological measurements

At each census date, after recording survival, the height of surviving seedlings was measured from the ground to the highest shoot tip above ground and the diameter was measured on the stem at 2 cm above ground with calipers. In July 2009, all the surviving seedlings were harvested after all the non-destructive measurements had

been taken. In the laboratory, each seedling was separated into leaf, stem and root fractions. Each fraction was oven-dried at 60 ℃ for 72 h and weighed to the nearest 0.001 g. Cumulative area of the total leaves of each seedling was measured on the fresh leaf material using a LI-3100C Area Meter (LI-COR, Lincoln, NE, USA). Specific leaf area (SLA) was then calculated as the ratio between cumulative leaf area and total leaf dry mass. Wood density (WD) was calculated as the ratio between stem dry weight and stem basal area. Leaf mass ratio (LMR) was calculated as the ratio between total leaf mass and total plant mass. Due to seedling mortality and physical damage, the total number of seedling for trait measurements was 192 for SLA, 175 for WD and 189 for LMR.

Data analysis

Mortality rate

The mortality rate, p_i, was estimated for each interval by dividing the number of deaths, y_i, in each interval by the number of survivors, n_i, at the beginning of each interval: $p_i = y_i / n_i$. The numbers of deaths are considered to be independent and binomially distributed. The mortality rate for the interval [t–1, t] can be related to the instantaneous mortality risk by the following expression:

$$p_i = 1 - e^{-\int_{t-1}^{t} \lambda_t dt}, \quad (1)$$

here λ is a hazard function, which is the probability that an event happens at time t given that it has not happened before. The hazard function of can be written as $\lambda_i(t) = \lambda_0(t) * e^{\sum \beta j}$, where i is the index of an individual, β_j's are the effects of age, growing season, species functional type, species identity, environmental covariates and functional traits and $\lambda_0(t)$ is a reference (baseline) hazard function free of the covariates. Approximating the integral in (1) using the mid-point rule (Candy, 1986) gives

$$p_i \approx 1 - e^{-\Delta t \cdot \lambda_{t-1/2}}, \quad (2)$$

where $\lambda_{t-1/2}$ is the instantaneous mortality risk at mid-time. Combining the equations (1) and (2), the systematic effects can be assessed by the expression

$$p_i = 1 - e^{-\Delta t \cdot e^{\sum \beta_j}}.$$

We fitted this model with GLMM (Generalized Linear Mixed Model) using a complementary log-log link, binomial distribution for the errors and an offset $\log_e(\Delta_t)$ (Candy, 1986, Egli & Schmid, 2001). In the full model, seedling age (log-scale), growing season, R:FR, LAI, PAR, soil properties (PH, total N, P and C), WD, SLA, LMR, site, plant functional type (broad-leaved evergreen, broad-leaved deciduous and conifer) and interactions between these terms were fitted as fixed terms, and quadrat and species identity were used as random terms. For environmental parameters R:FR, LAI, PAR, PH, total N, P and C, we used quadrat means, whereas for plant functional traits WD, SLA and LMR, we used species means.

After running the full model, we updated the model by removing non-significant fixed terms and interactions between them. We reported only significant effects and R:FR, because light condition was the main factor of interest in our study. We chose R:FR as an indicator of light availability for two reasons. First, it was measured above each individual instead of being measured for each quadrat (as done in the measurement of LAI). Second, R:FR was expected to be more reliable than PAR as an indicator of the relative light condition experienced by plants as the latter showed large daily variation.

Growth rate

Linear regression between stem volume and seedling biomass were calculated for each of the three plant functional types (evergreen broad-leaved, deciduous broad-leaved and evergreen coniferous species) as the two have been shown to be highly correlated (Kohyama & Hotta, 1990). These regressions were used to estimate seedling biomass over time from the non-destructive measurements. We then calculated the relative growth rate (RGR) from these estimated biomass values as

$$RGR = \frac{\log(M_2) - \log(M_1)}{T_2 - T_1}, \qquad \text{(Eq. 1)}$$

where M_1 and M_2 stand for seedling biomass before and after a census interval and T_1 and T_2 stand for time before and after the interval. We fitted a mixed-effects model of RGR with a restricted maximum likelihood (REML) approach. In the model, seedling age (log scale), growing season, site, plant functional type (broadleaved-evergreen, deciduous, and conifer), wood density, SLA, LMR, soil properties (PH, total N, P and C), R:FR, LAI, PAR and interactions between these terms were fitted as fixed terms,

and quadrat and species identity were used as random terms. Similar to the analysis with mortality, we used quadrat means for environmental variables. For functional traits, we used both species means and individual traits directly measured at the final harvest. All analyses were carried out with GenStat software (13th edition, VSN International Ltd, UK).

For simplicity, we refer to the census intervals August 2007–March 2008 as first, March 2008–August 2008 as second, August 2008–January 2009 as third, and January 2009–July 2009 as fourth interval. The first and third interval mostly fell outside the growing season while the second and fourth intervals mostly covered the growing season (Chen, 2000).

Results

Seedling mortality

The mean percentage of surviving seedlings from transplanting to the four census dates was 88%, 57%, 50% and 37%, respectively. Survivorship of seedlings differed between plant functional types, with evergreen broad-leaved species having the highest and conifers having the lowest values (Fig. 1).

Mortality rate did not significantly change along the gradient of R:FR (Table 3, Fig. 4). Instead, log-age, season and species-mean wood density (WDspec) had mainly effects on mortality rates (Table 3). Mortality rate increased over time (log-age) and was higher during the growing season (Fig 3(a)). Mortality rate was negatively related to WDspec (Table 3, Fig 5(a)). There was also significant interaction between WDspec and nitrogen content in soil showed that seedling mortality decreased more rapidly with increasing wood density on soils with higher soil nitrogen. Plant functional type (Conifer and ED) were shown to be significant when they were fitted before WDspec in the model, which was in accordance with our observations from Fig. 1. When these terms were fitted after WDspec, they became insignificant (Table 3) which showed the different mortality rate between functional types could be explained by the differences in species-specific wood density. The other two traits SLA and LMR were not related to mortality.

Relative growth rate (RGR)

On average, evergreen species had lower relative growth rates than deciduous species.

The growth of deciduous species was strongly season-dependent. For example, during the second growing season, *Choerospondias axillaris* reached a RGR as much as 6 mg/day while during non-growing seasons its RGR was extremely low, even showing negative values (Fig. 2).

RGR was significantly influenced by seedling age, season and their interaction. As expected, higher RGRs were observed during than outside the growing season, especially in the first year (Table 4, Fig. 3(b)). None of soil nutrient or light parameters was related to RGR when tested in a overall model, whereas wood density (individual mean) was again the most important trait influencing seedling growth rate (Table 4). However, after conducting separate analysis for each interval, we found in the 4th interval (January 2009–July 2009), RGR decreased with decreasing soil nitrogen and R:FR. (Appendix B).

Functional traits

All of the functional traits we studied showed considerable variation among species and individuals. Overall, 3-fold variation among species was found in specific leaf area (SLA, 80–264 cm^2/g), leaf mass ratio (LMR, 15–40%) and wood density (WD, 0.19–0.61 g/cm^3) (Table 1). In comparison, 10-fold variation was found among individuals in these traits (SLA, 29–316 cm^2/g; LMR, 6–60%; WD, 0.11–1.01 g/cm^3).

WD and LMR showed higher value in broad-leaved evergreen than deciduous species while SLA showed the opposite pattern, which indicated that evergreen broad-leaved species had denser wood, thicker leaves and allocated more biomass to leaves than did deciduous broad-leaved species. Light or soil parameters exerted little impact on any of the functional traits except for LMR, where the interaction between soil nitrogen and plant functional type was significant: in deciduous species, LMR decreased as soil nitrogen increased while in both evergreen broad-leaved and conifer species, LMR increased as soil nitrogen increased (Table 5).

Mortality and growth rate

The mortality rate and RGR between species was not related in the first year (Fig. 6(a)), while in the second year they were positively correlated (p=0.02, r=0.605; Fig. 6(b)). No significant relationship was detected at within-species level (Fig. 6).

Discussion

We examined the survival and growth rate of seedlings growing in the forest understory. In contrast to the shade-house experiment (Chapter1), environmental conditions in natural habitats are strongly heterogeneous. As shown in Table 2, seedlings in our transplanting experiments experienced not only variation in light availability, but also in multiple other resources, including soil nitrogen, phosphorous and soil moisture. Results from Principal Component Analysis (PCA) on the eight environmental variables we measured suggested soil nitrogen content may have confounding effect on seedling performance. The first axis from PCA result represented a combined gradient of soil nitrogen content, soil moisture, R:FR and LAI (Appendix A). Thus, open quadrats had not only more light but also tended to be poorer in nitrogen and carbon. The lower nutrient availability may have limited seedling growth and increased mortality in the high light. Nonetheless, the main results did not change when soil parameters were fitted as covariants, thus in the following paragraphs, we discuss the potential explanations for the observed seedling performance pattern without much consideration into the variation of soil nutrients.

Factors influencing seedling mortality

Studies on seedling shade-tolerance usually report increased seedling mortality with decreasing light availability (Bloor, 2003, Kitajima, 1994, Poorter, 1999). However, different from expectation, our results showed that at least during the first two years after seedling establishment, low light availability did not increase the mortality rates of seedlings. There are three major possible explanations.

First, in contrast to the present study, previous studies were conducted in shade houses, which are useful in interspecific comparisons of shade-tolerance, but the may not reflect field conditions. In shade-house experiments, seedlings are largely protected from herbivory, pathogen attack and mechanical damage, which are major causes of seedling mortality in the forest understory (Augspurger, 1984a). This was also the case in our study. We found species-mean wood density, which should be negatively related with a species' vulnerability to pathogens (Augspurger, 1984b), was also negatively related to seedling mortality (Fig. 5(a)). Shade-house experiments also keep seedlings from competing with other plants. However, in our study at

natural field sites we found greater seedling mortality during the growing seasons (Fig. 3(a)) when competition between individual plants is most severe (Harper, 1977).

Second, the natural light availability in a subtropical forest understory is relatively high compared to shade-houses mimicking the light condition at the bottom of a dark tropical forest, which is in the order of 0.5–2% of above-canopy light (Chazdon, 1988, Clark *et al.*, 1996). In the understory of our forest, light availability ranged from 3–17% of above-canopy light. Furthermore, light condition varied seasonally in this subtropical forest where the canopy consists of winter-deciduous and evergreen species. Light availability was much higher in winter as all the winter-deciduous trees have shed their leaves. The low carbon balance of an evergreen seedling that was shaded during the growing season can be compensated during winter before it reaches the point of negative carbon balance which will lead to mortality.

In summary, our results suggest that besides light availability, competition and traits that improve species resistance to abiotic and biotic stresses can be important factors influencing the survival of seedlings growing in the understory of a subtropical forest.

Factors influencing seedling growth

Interestingly, light availability did not increase seedling growth during the first three census intervals. Only during the last interval (1.5 years after transplantation of seedlings to the field), RGR was significantly higher in higher light. At this time, the ranking of species with regard to RGR was reversed along the R:FR gradient. That is, species growing faster than others under high R:FR grew slower than others under low R:FR (Fig. 7). The rank reversal in RGR has often been suggested as one of the mechanisms of niche differentiation between light-demanding and shade-tolerant species and explanation of species coexistence along a light gradient. This suggestion is based on the observation that the mass-based net photosynthetic rates of shade-tolerant species exceed those of shade-intolerant species in shade, whereas the reverse is the case at high irradiance (Givnish, 1988, Latham, 1992, Pacala, Canham, Silander *et al.*, 1994). However, this reasoning has been questioned because other studies of a larger number of species have failed to detect substantial rank reversals

between gap and shade (Kitajima, 1994, Poorter, 1999, Veneklaas & Poorter, 1998). Our results provide a possible solution for the conflict, namely that the rank reversal between species can be age-dependent (Niinemets, 2006, Perez-Ramos, Gomez-Aparicio, Villar *et al.*, 2010). For example, seedlings of both light-demanding and shade-tolerant species may initially mainly need to survive the above-mentioned non-light related stresses and thus have similar responses to shade and light. After this initial phase, light may become the dominant environmental factor for them and lead to the expression of strategy differences among functional groups (Sack & Grubb, 2001). It has also been reported that leaf mass per area, the inverse of SLA, increases with age more rapidly in shade-intolerant species under low light condition so that these plants have lower photosynthetic capacity and therefore smaller whole-plant growth rate in the shade than shade-tolerant ones (Niinemets, 2006).

The relation of mortality and growth with functional traits

We found that species-mean wood density was the single best predictor of seedling mortality in the understory of a subtropical forest (Table 3, Fig. 5(a)), but it was not related to growth rate. Instead, individual-mean wood density was negatively related to seedling growth rate (Table 4). Our results show that WD is an important functional trait tightly correlated with seedling performance. Similar patterns have been found for large trees (King, Wright & Connell, 2006, Muller-Landau, 2004, Poorter, Wright, Paz *et al.*, 2008), which is in line with resistance to physical damage and higher construction cost associated with dense wood.

Interestingly, we did not find any relation between SLA and seedling growth although such a relation has been regarded as a major factor associated with variation in RGR (Poorter & Remkes, 1990, Veneklaas *et al.*, 1998). Deciduous species did have larger SLA than evergreen species, but RGR was not different between these two functional types. Likewise, LMR, the proportional biomass allocated to leaves, was not related to seedling growth nor to seedling survival. Again, these findings suggest that in a subtropical forest understory, functional traits that enhance light interception may not be crucial for the performance of seedlings during the initial establishment phase. Rather, WD, which strengthens seedlings' resistance against other stressors, may be more important for survival and growth during this phase in the forest

understory.

The relation between mortality and growth rate

In this study, we did not find a previously described trade-off between low-light survival and high-light growth rate (Kitajima, 1994, Kobe, Pacala, Silander *et al.*, 1995). However, there was a general inter-specific relation between mortality rate and RGR which was affected by seedling age. In the second year, the inter-specific relation between mortality rate and RGR was positive, while almost half of the species showed negative relations between mortality rate and RGR within species in the second year (data not presented). The interspecific trade-off reflected genetic differences among species, because the study design avoided confounding species and field conditions (Schmid, 1992). In contrast, the high growth–low mortality within-species tradeoff most likely reflected local environmental differences: when the local environment was good, seedlings had both high growth rate and low mortality and vice versa. Our results, in accordance with previous studies (Seiwa, 2007), suggest that genetic differences allow species with different strategies to coexist in a heterogeneous habitat, whereas phenotypic plasticity allows individual plants to fully utilize resource patches within it.

Conclusions

The seedling stage of subtropical shrubs and trees is very likely more vulnerable to disturbance and environmental conditions than the seed or adult tree stage. It is thus particularly important to study the survival and growth of seedlings in the forest understory to predict species composition in the longer term. With our 2-year field transplant experiment in a subtropical forest understory, we found that light availability was not the single critical factor determining seedling performance. Rather, seasonal competition and functional traits which enhanced a seedlings' resistance to multi-level stresses in the understory appeared to be of even greater importance at least during the initial establishment phase. Nutrient availability for plant growth is lower in forest gap than in deep understory, as shown in our study (Appendix A), due to the more severe competition for nutrients in high-light conditions (Tilman, 1993). Furthermore, plant growth is more limited by nutrient in high light than low light (Tilman, 1993). The compensatory effect of high nutrient in

low light can also be an explanation for little effect of light on plant growth. However, our study does suggest that after this initial phase, light-demanding and shade-tolerant strategies are deployed by different species and that this niche differentiation may increase species coexistence in a heterogeneous habitat, where the former grow relatively faster in patches with better light conditions and the latter grow faster in patches with lower light.

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Tables

Table 1: Species taxonomy, functional type and species-means of functional traits with standard error of the means (no standard error is shown when there was only one plant survived at the time of trait measurement). WD = wood density, SLA = specific leaf area, LMR = leaf mass ratio.

Species	Family	Conifer	Functional type	WD (g/cm^{-3})	SLA (cm^2/g)	LMR
Alangium chinense	Alangiaceae	no	deciduous	0.28±0.14	264±150	0.17±0.11
Aralia chinensis	Araliaceae	no	deciduous	0.42±0.22	124±89	0.29±0.11
Camellia oleifera	Theaceae	no	evergreen	0.43±0.26	134±103	0.35±0.13
Castanea henryi	Fagaceae	no	deciduous	0.38±0.06	165±54	0.20±0.06
Choerospondias axillaris	Anacardiaceae	no	deciduous	0.24	134	0.41
Cryptomeria fortunei	Taxodiaceae	yes	evergreen	0.36±0.16	80±44	0.39±0.14
Diospyros cathayensis	Ebenaceae	no	evergreen	0.49±0.33	109±130	0.24±0.09
Diospyros kaki var. *silvestris*	Ebenaceae	no	deciduous	0.33±0.21	215±209	0.22±0.12
Lindera communis	Lauraceae	no	evergreen	0.61±0.37	162±207	0.35±0.14
Lindera limprichtii	Lauraceae	no	evergreen	0.50±0.4	154±135	0.32±0.12
Phoebe microphylla	Lauraceae	no	evergreen	0.56±0.3	159	0.33±0.11
Phoebe zhennan	Lauraceae	no	evergreen	0.52±0.35	137±73	0.36±0.10
Pinus massoniana	Pinaceae	yes	evergreen	0.20	143	0.27
Toxicodendron succedaneum	Anacardiaceae	no	deciduous	0.26±05	104±33	0.28±0.13

Table 2: Abiotic parameters measured in each field quadrate, including soil parameters N, C, P (total soil nitrogen/carbon/phosphors), PH value, soil water content, and parameters indicating light conditions in each quadrate R:FR (red:far-red ratio), PAR (photosynthetic active radiation (μmol m^{-2} s^{-1})) and LAI (leaf area index). Standard error of the quadrate-mean is shown for R:FR and PAR.

Unit	Site	N (g/kg)	C (g/kg)	P (g/kg)	PH	Soil water content (%)	R:FR	PAR	LAI
1	A	2.4	31.5	0.36	4.48	29.6	0.87±0.2	3.64±1	1.8
2	A	2.4	31.3	0.29	4.35	41.1	1.0±0.1	8.37±4.11	2.55
3	A	1.6	19.2	0.44	5.47	24.4	2.63	85.5	0.1
4	A	2.8	40.6	0.22	4.60	39.0	0.8±0.1	1.76±0.72	2.47
5	A	3.3	51.4	0.24	4.12	43.5	0.9±0.03	6.53±2.78	2.3
6	A	4.2	61.8	0.34	4.68	49.3	2.63	85.5	0.1
7	B	2.9	36.6	0.38	4.70	37.0	0.88±0.03	7.27±1.73	1.9
8	B	2.8	30.1	0.34	5.52	42.4	0.9±0.15	16.58±2.43	2.49
9	B	2.6	34.6	0.34	4.49	34.6	0.79±0.04	2.12±0.86	2.13
10	B	1.5	13.7	0.46	5.81	29.7	2.63	85.5	0.1
11	B	1.9	19.4	0.30	5.06	32.4	0.91±0.04	8.48±2.12	2.22
12	B	2.2	33.8	0.78	4.01	34.1	1.03±0.02	112.1±17.2	1.41

Table 3: Significance test of factors influencing mortality rate of seedlings. logage = log-scale seedling age, R:FR = red: far red ratio, N = total nitrogen content in the soil, WDspec = species-mean of wood density, ED = evergreen/deciduous. d.d.f. = denominator degrees of freedom. Numerator degrees of freedom = 1.

Fixed term	F statistic	d.d.f.	*p*
logage	37.03	489.8	<0.001***
Season	18.9	483.5	<0.001***
Site	8.88	4.8	0.033*
R: FR	0.35	484.2	0.556
N	0.63	482.8	0.427
WDspec	20.16	9.4	0.001***
N.WDspec	13.23	487	<0.001***
Conifer	0	9.4	0.999
ED	3.88	9.1	0.08

Table 4: Significance test of factors influencing relative growth rate of seedlings. The results was obtained with a restricted maximum likelihood (REML) approach. In the model, log-scale seedling age (logage), growing season (season), site, evergreen or deciduous (ED), conifer, individual-mean of wood density (WD), individual-mean of specific leaf area (SLA), individual mean of leaf mass ratio (LMR), quadrate-mean of total nitrogen content in the soil (N), quadrate-mean of red: far red ratio (R:FR) and interactions between these terms were fitted as fixed terms while quadrate and species identity were used as random terms. d.d.f. = denominator degrees of freedom. Numerator degrees of freedom = 1. ***: $P < 0.001$; **: $P < 0.01$; *: $P < 0.05$.

Fixed term	F statistic	d.d.f.	*p*
logage	0.16	594.1	0.689
Season	16.15	593.3	<0.001***
Site	2.22	5.7	0.189
Conifer	2.75	8.7	0.132
WD	13.07	587.7	<0.001***
N	0	8.2	0.955
R:FR	0.33	7.8	0.579
logage x Season	30.5	593.2	<0.001***
logage x site	0.14	593.2	0.704
Season x site	2.93	593.1	0.087
logage x Conifer	2.75	599.3	0.098
Season x Conifer	3.35	594.6	0.068
Conifer x ED	0.57	10.9	0.467
logage x WD	8.41	593.6	0.004**
Season x WD	3.46	593.2	0.064
logage x N	0.01	594.2	0.912
Season x N	2.9	593.3	0.089
logage x R:FR	1.81	594.8	0.179
Season x R:FR	11.17	593.5	<0.001***

Table 5: Result from general mixed model of the three functional traits wood density (WD), specific leaf area (SLA) and leaf mass ratio (LMR) using site, conifer (Con), evergreen or deciduous (ED), total nitrogen content in the soil (N), red: far red ratio (R:FR) as explainatory factors. ***: $P < 0.001$; **: $P < 0.01$; *: $P < 0.05$.

	WD	SLA	LMR
site	0.875	0.472	0.912
Con	0.182	0.024*	0.119
N	0.794	0.768	0.632
R:FR	0.063	0.464	0.052
Con.ED	0.003**	0.013*	0.01*
site.N	0.9	0.299	0.721
Con.N	0.613	0.953	0.543
site.nf	0.425	0.807	0.403
Con.nf	0.441	0.646	0.156
Con.ED.N	0.834	0.113	0.012*
Con.ED.nf	0.551	0.186	0.86

Fig. 1. Percentage of seedling survival at each census. The total number of seedlings transplanted at the beginning of study (August 2007) is 20. Species are listed from left to right according to plant functional type: broad-leaved evergreen species (from *Camellia oleifera* to *Phoebe zhennan*), deciduous species (from *Alangium chinense* to *Toxicodendron succedaneum*) and coniferous species (*Cryptomeria fortunei* and *Pinus massoniana*).

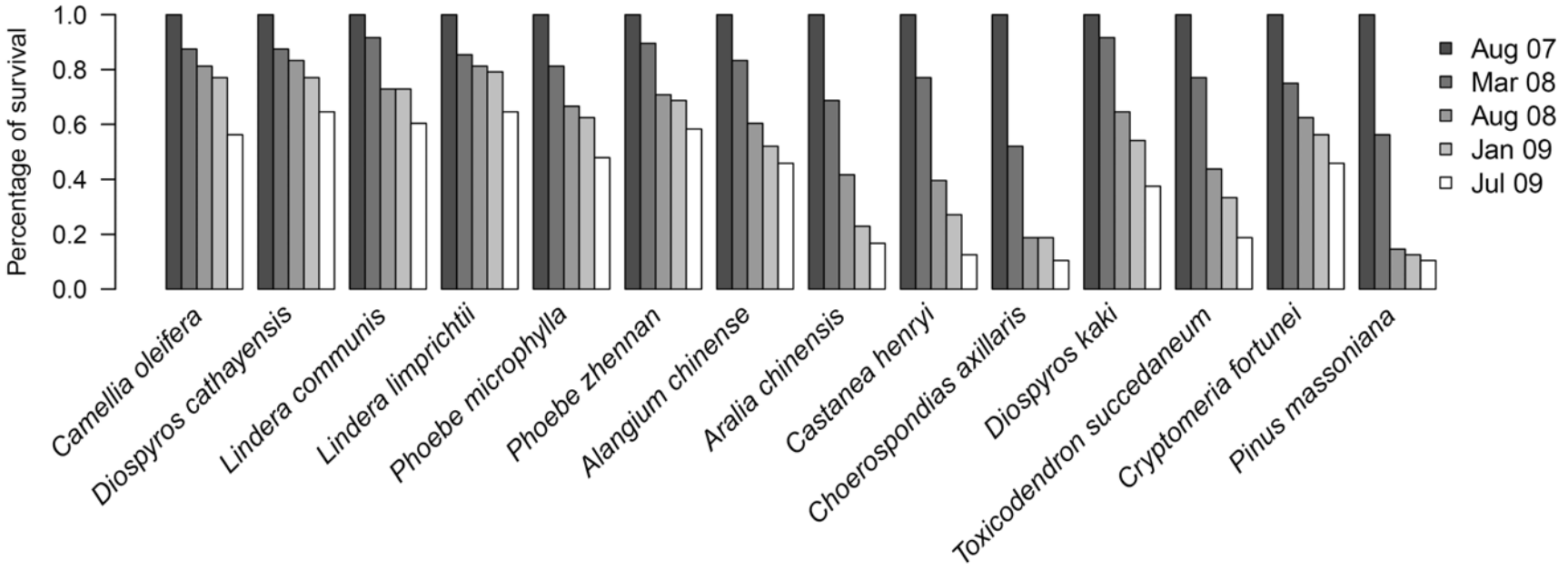


Fig. 2. Relative growth rate (RGR) of each species over the study period. Species are listed from left to right according to plant functional type: broad-leaved evergreen species (from *Camellia oleifera* to *Phoebe zhennan*), deciduous species (from *Alangium chinense* to *Toxicodendron succedaneum*) and coniferous species (*Cryptomeria fortunei* and *Pinus massoniana*).

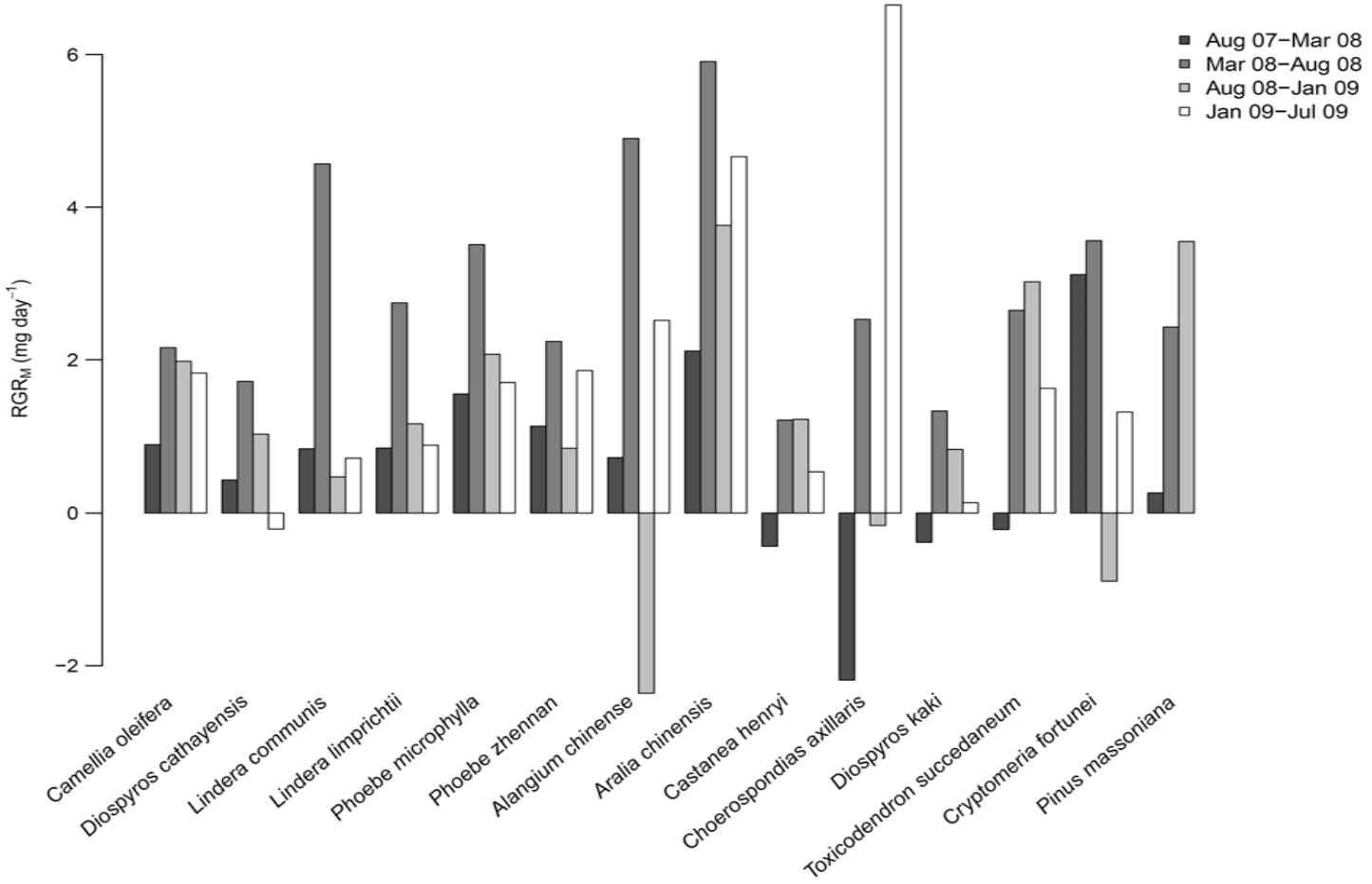


Fig. 3. Average mortality rate (a) and relative growth rate (RGR) (b) during the four census intervals. Points showed the mean mortality rate or RGR over census intervals and error bars showed the standard error of the means.

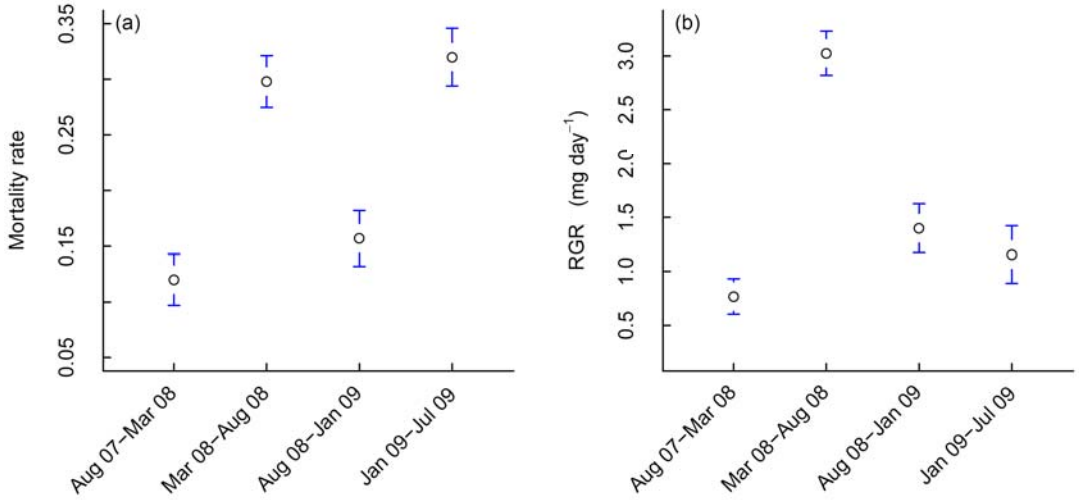


Fig. 4. Predicted mortality risk along the gradient of R:FR. Each line shows the performance of each species. Species are classified into the three functional types broad-leaved deciduous, broad-leaved evergreen and coniferous species, which are denoted as solid, dashed and dotted lines, respectively.

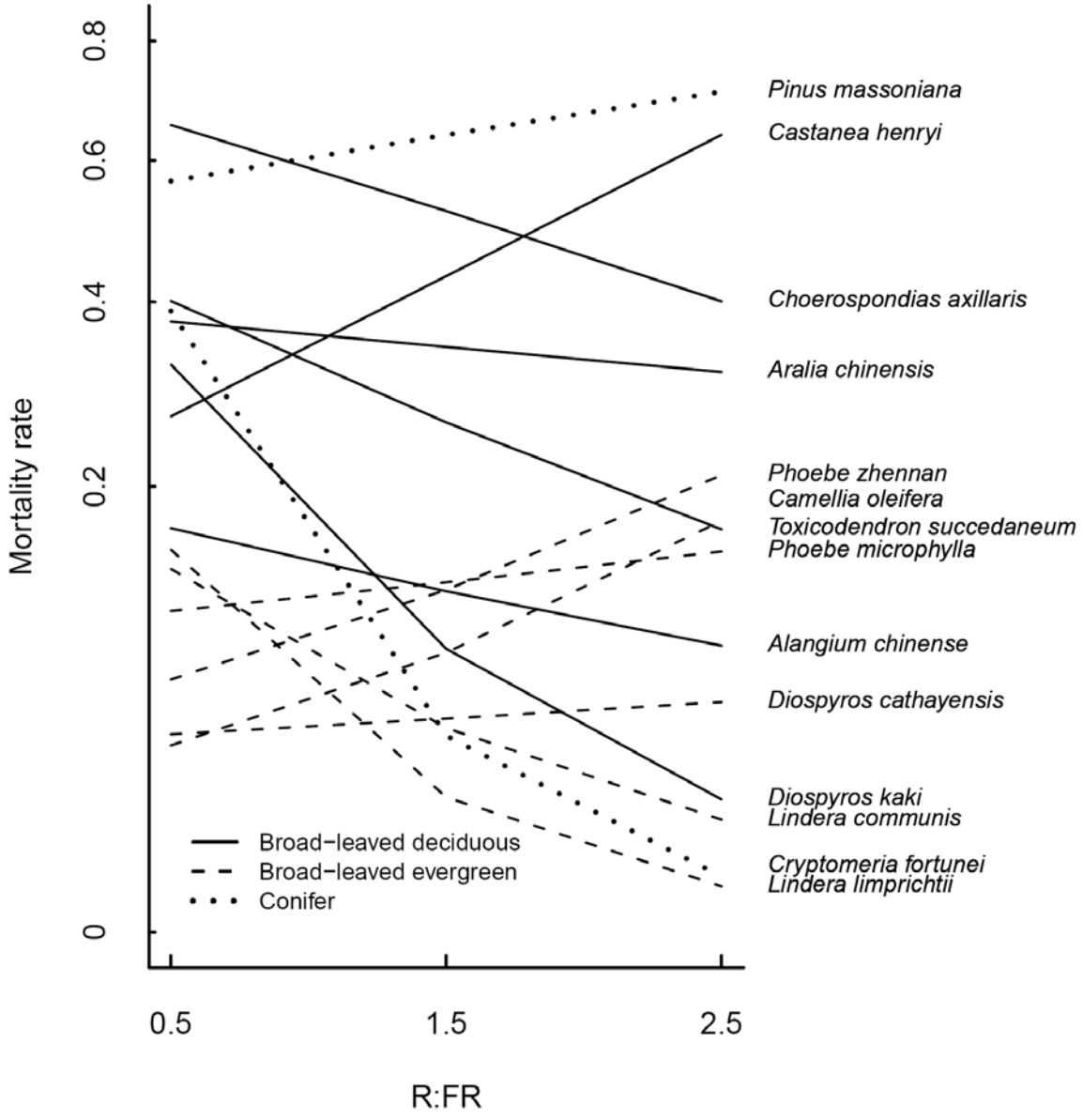


Fig. 5. Relationships between (a) seedling mortality rate and (b) relative growth rate (RGR) and species-mean wood density (WDspec). Species were classified into the three plant functional types broad-leaved deciduous (d), evergreen (e) and conifers (c). Solid lines show predictions with WDspec included in the model and dashed lines show the predictions calculated with full model. Error bars showed the standard error of the mean.

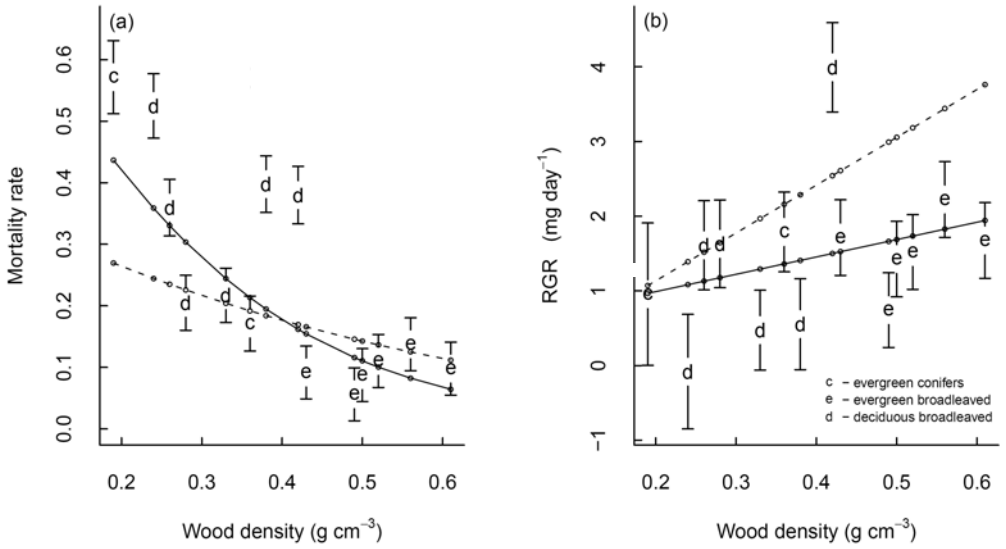


Fig. 6. Relationships between relative growth rate (RGR) and mortality rate from August 2007 to August 2008 (a) and from August 2008 to July 2009 (b). Species were classified into broad-leaved deciduous (d), evergreen (e) and conifers (c). Error bars showed the standard error of the mean. Solid lines showed the regression line of the positive correlation between mortality rate and RGR between August 2008 and July 2009.

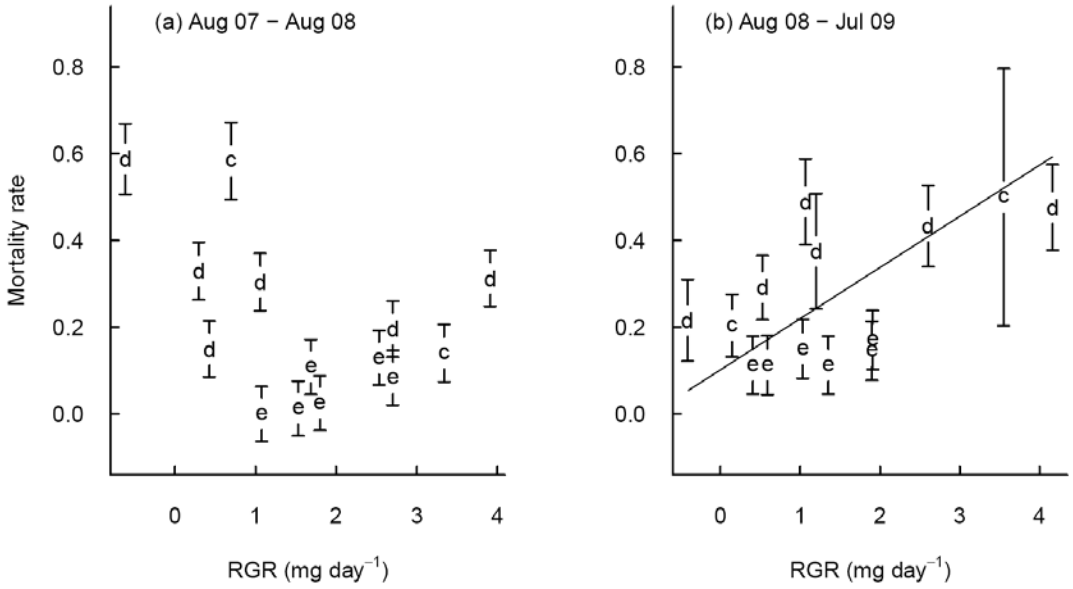
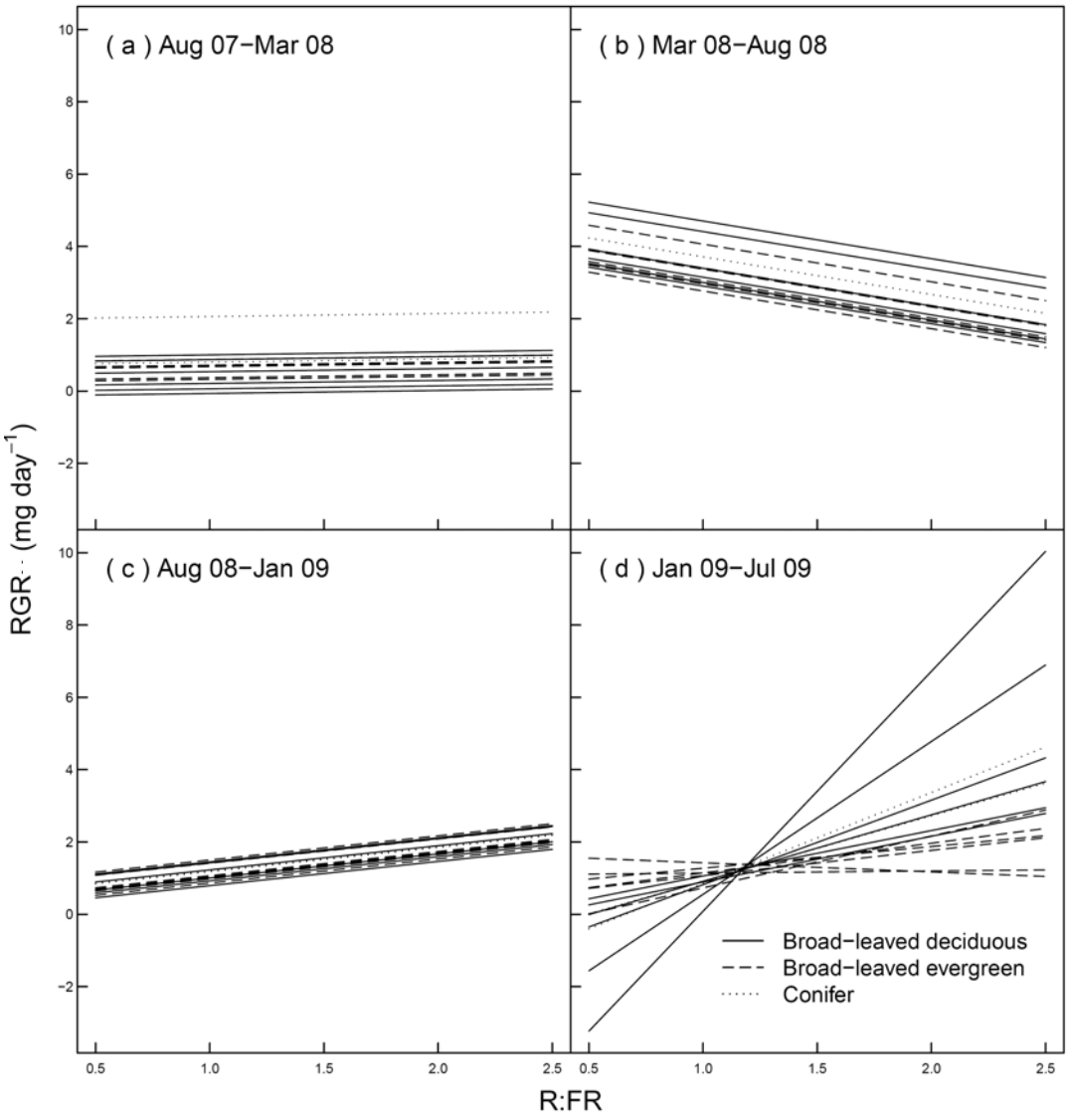
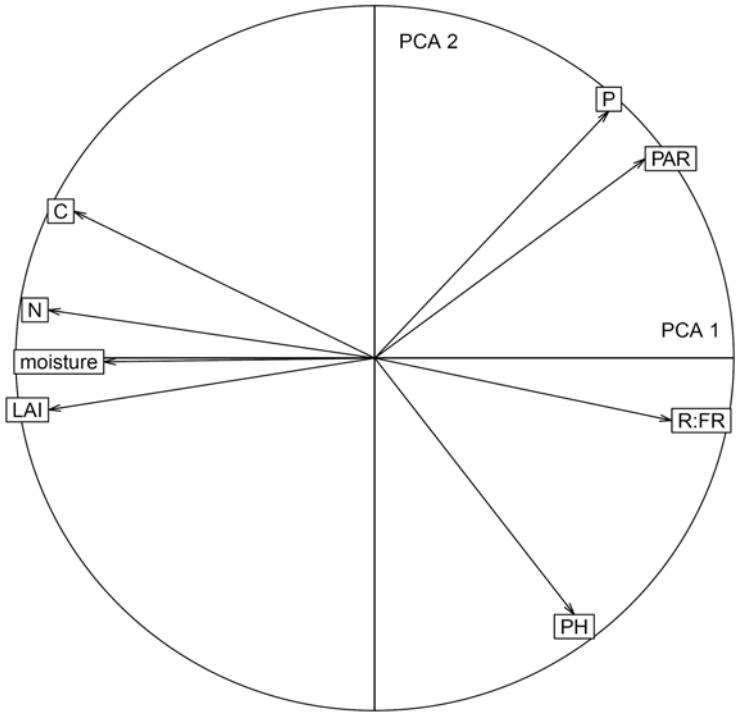


Fig. 7. Predicted relative growth rate of biomass (RGR) along the gradient of R:FR. (a) August 07–March 08; (b) March 08–August 08; (c) August 08–January 09; (d) January 09–July 09. Each line shows the performance of each species. Species are classified into the three functional groups broad-leaved deciduous, broad-leaved evergreen and coniferous species, which are denoted as solid, dashed and dotted lines, respectively.



Appendix A: Result of Principle Component Analysis (PCA) of environmental parameters, including including soil parameters N, C, P (total soil nitrogen/carbon/phosphors), PH value, soil water content, and parameters indicating light conditions in each quadrate R:FR (red:far-red ratio), PAR (photosynthetic active radiation) and LAI (leaf area index).



Appendix B: Results from significance test of factors influencing RGR during each census interval. Con = conifer/angiosperm, ED = evergreen/deciduous, N = total nitrogen content in the soil, R:FR = red: far red ratio, WD = wood density.

	Aug 07–Mar 08	Mar08–Aug 08	Aug 08–Jan 09	Jan 09–Jul 09
Con	<0.001***	0.609	0.319	0.253
Con.ED	0.794	0.207	0.546	0.717
N	0.205	0.83	0.62	<0.001***
R:FR	0.172	0.421	0.881	0.004**
WD	0.89	0.017*	0.326	<0.001***

CHAPTER 4

Decomposing variance and covariance in functional traits in a Chinese subtropical forest

Xuefei Li , Kequan Pei, Marc Kéry and Bernhard Schmid

Abstract

Functional traits, properties of organisms correlated with ecological performance, play a central role in processes of community assembly. To gain a better understanding of these processes, it is therefore necessary to understand the factors influencing trait variation and covariation within communities in an ecological and evolutionary context. We studied the three leaf traits leaf half-life (LHL), leaf mass per area (LMA) and nitrogen concentration in green leaves (N_{green}) and the wood trait wood density (WD) in 295 individuals belonging to 45 tree or shrub species in a Chinese subtropical forest from September 2006 to January 2009. Using multilevel ANOVA and decomposition of sums of products, we estimated the amount of trait variation and covariation among taxa, functional types (deciduous vs. evergreen), growth forms (trees vs. shrubs), individuals and seasons. We also examined phylogenetic signal and, using phylogenetically independent contrasts, the evolutionary coordination of these traits. For single traits, the variation between functional types and among species was large, but only LMA and N_{green} varied significantly among families and thus showed phylogenetic signal. Apart from seasonal differences, trait variation within species was small. We did not find any trait variation related to variation in soil conditions underneath the measured individuals. For pairs of traits, variation between functional types and among species was again large. This reflected a strong evolutionary coordination of the traits, with LMA, LHL and WD being positively correlated among each other and negatively correlated with N_{green}. This integration of traits was consistent with the global leaf economics spectrum and was not influenced by phylogenetic history. Trait coordination within species was weak, indicating that the observed trait spectrum was not accentuated by environmental or developmental variation among individuals. Our findings suggest that in a woody plant community, variations in functional traits reflect integrated strategies of species, which can be placed along a spectrum from deciduous species with short-lived, thin, high-nitrogen leaves and light wood to evergreen species with long-lived, thick, low-nitrogen leaves and dense wood. This within-community spectrum corresponds well to the reported global leaf economics spectrum, extended by the dimension of wood density.

Introduction

Functional traits play a central role in ecological processes that influence species distribution and community organization (McGill, Enquist, Weiher *et al.*, 2006, Westoby & Wright, 2006). From alpine tundra to tropical rain forests, the amount of interspecific functional trait variation found in nature is enormous. For example, leaf nitrogen, leaf mass per area and leaf life-span vary 10- to 100-fold across different communities (Reich, Walters & Ellsworth, 1992, Wright, Reich, Westoby *et al.*, 2004). Plant functional traits do not vary independently. Rather, there is a continuum of leaf carbon and nitrogen investment strategies, forming a leaf economics spectrum which runs from species with inexpensive, short-lived leaves with rapid returns on carbon and nutrient investments to species with costly, long-lived leaves with slow returns (Reich, Walters & Ellsworth, 1997, Wright *et al.*, 2004). A further coordination axis may relate these leaf traits to wood traits (Bucci, Goldstein, Meinzer *et al.*, 2004, Ishida, Nakano, Yazaki *et al.*, 2008, Santiago, Goldstein, Meinzer *et al.*, 2004). Coordinated investments in leaf and wood tissue as a plant strategy could explain why fast-growing species tend to have thin leaves and low wood density, and vice versa. The extensive interspecific comparison has advanced our understanding in evolutionary adaptation of species in contrasting environments, as each present species must contain a trait combination which is ecologically competent. However, studies of trait variation along environmental gradients often focus on species- or community-mean trait values with little attention to within-species variation (Ackerly & Cornwell, 2007, Shipley, Vile & Garnier, 2006), which is insufficient in studies within communities. because processes that drive community assembly (such as environmental filtering) may act on functional traits irrespective of species identity (McGill et al., 2006, Messier, McGill & Lechowicz, 2010). This does not mean that species are indistinguishable from one another but that the trait variation and covariation within species can be large compared with trait variation and covariation between species. Therefore, an analysis of multilevel variation in traits and coordination between trait-pairs within a forest community may facilitate our understanding of processes involved in community assembly. In the present study we partitioned trait variation and covariation into the following components: a) among the functional types deciduous and evergreen and among the growth forms xxx, b) among families and among species within families (i.e. taxonomy), c) among individuals and d) between early and late growing season. To do this partitioning we

used multilevel analysis of variance (multilevel ANOVA) for trait variation and an ANOVA-like decomposition of sums of products for trait covariation.

A long-term aim of plant ecology has been to understand how local communities are assembled from the available species pool (Diamond, 1975, Weiher, Clarke & Keddy, 1998, Weiher & Keddy, 1999). Community assembly is assumed to represent the outcome of two opposing forces: abiotic controls (environmental filtering) that tend to constrain species living in a common environment within certain limits, and internal forces (niche partitioning, limiting similarity or complementarity) that prevent coexisting species from being too similar (Grime, 2006, Weiher et al., 1998). On the one hand, at any particular site with homogeneous environment, a hierarchical set of filters including climatic conditions, disturbance regimes and biotic interactions can be found, and these filters determine the optimal trait values in a community (Diaz, Cabido & Casanoves, 1998, Keddy, 1992, Schmid, Joshi & Schlapfer, 2001). On the other hand, high levels of trait disparity due to limiting similarity of species are also often observed within communities (Ackerly, Knight, Weiss *et al.*, 2002, Cornwell & Ackerly, 2009, Wright *et al.*, 2004). Whether plant traits vary in a coordinated way, whether plants utilize different strategies to coexist in a community and how taxonomy, environmental heterogeneity and functional groups influence on present-day trait combinations are essential questions in understanding community assembly.

Therefore, we measured four plant functional traits among 45 co-occurring tree and shrub species in a Chinese subtropical forest and partitioned the trait variation and covariation into the following components: a) between functional types (deciduous vs. evergreen) and between growth forms (tree vs. shrub), b) among families and among species within families (i.e. taxonomy), c) among individuals within species and d) between early and late growing season. To do this partitioning we used multilevel analysis of variance (multilevel ANOVA) for trait variation and an ANOVA-like decomposition of sums of products for trait covariation. We chose the four functional traits leaf half-life (LHL), leaf mass per area (LMA), leaf nitrogen concentration (N_{green}) and wood density (WD). LMA is the reciprocal of specific leaf area and represents the light-intercepting area of a leaf per unit mass, has been shown to relate to many important physiological characteristics such as leaf nutrient concentration, photosynthetic capacity and plant relative growth rate (Wright *et al.*, 2004). LMA is expected to be related to LHL; and LHL is expected to be positively

correlated to N_{green} (Reich *et al.*, 1992, Reich *et al.*, 1997, Wright *et al.*, 2004). However, these relationships have not been rigorously tested so far in part due to the amount of field work required to estimate LHL. In the present study, LHL was estimated via leaf demography. These three leaf traits used to describe a leaf economics spectrum are expected to be related to WD, a functional trait of central importance because of its association with hydraulic properties and rates of plant growth and mortality (Chave, Coomes, Jansen *et al.*, 2009, Wright, Ackerly, Bongers *et al.*, 2007).

It is worth noting that, as traits bear legacy along the tree of life, the variance and covariance pattern in traits may not simply be a consequence resulting from ecological processes, but rather due to common ancestry. In this paper we used Blomberg's K (Blomberg, Garland & Ives, 2003) as an estimate of phylogenetic signal in individual traits and phylogenetically independent contrasts (PICs; Felsenstein, 1985) for the analysis of relationships between traits to account for potential phylogenetic confounding among species

Materials and Methods

Study area and plant species

The study was conducted in a secondary broad-leaved and coniferous mixed subtropical forest in Dujiangyan, Sichuan province, SW China. With the rising slopes of the Qinghai-Tibet plateau to the west and the fertile agricultural plains of the Sichuan basin to the east, the Dujiangyan area is one of eleven biodiversity hotspots in China (Chen, 2000). The climatic conditions are typically subtropical with a dry winter (November–April) and a warm and rainy summer (May–October). The annual average temperature is 15.2 °C and July average temperature is 25 °C. The mean annual precipitation is 1341 mm and the annual average relative humidity is above 80 % (Chen, 2000).

The study site covers approximately 22 ha (31˚03'43"–31˚04'03" N, 103˚42'55"–103˚43'52" E), within an altitude range of 693–830 m. Previous vegetation survey shows there are 158 species of broad-leaved evergreen, deciduous and coniferous trees and shrubs coexist in the forest (Du, unpublished data). The canopy is dominated by *Castanopsis fargesii*, *Betula luminifera, Quercus serrata* and

Quercus variabilis. Species nomenclature follows "Flora of China" (ECCAS, 1974-1999). *Camellia oleifera* and *Eurya alata* are the most abundant shrub species. The dominant soil types are Leptosols, Regosols and Cambisols from loess-like material, with an average nitrogen concentration of 0.29 % and organic matter concentration of 8.56 %.

We selected 45 woody angiosperm species representing 19 families, which were commonly found in the forest community (Table 1). They were classified by functional type: deciduous (20 species) and evergreen (25 species) and by growth form: trees (34 species) and shrubs (11 species).

Measurements

Soil properties

We extracted one soil core (10 cm deep, 3 cm diameter) beneath 132 individual plants from 12 deciduous and 24 evergreen species in August 2009. These soil samples were oven-dried, ground and analyzed for total N concentration and organic matter concentration (FOSS 2200, Foss Tecator AB, Sweden) in the Institute of Botany, Chinese Academy of Sciences, Beijing, China.

Leaf mass per area and leaf nitrogen content

In September 2006, we randomly selected 3–6 individuals from each species and marked them with aluminum tags. We collected 5–8 fully expanded leaves from the middle of the leaf crown of each individual. For tall trees (height > 15 m) in which the middle of the crown could not be reached, leaves were collected from the bottom of the crown. Only current-season, fully expanded leaves at the edge of the crown were included in each sample. We used a LI-3100C Area Meter (LI-COR company, Lincoln, NE, USA) to determine the cumulative area of each sample of green leaves excluding petioles. The samples were dried at 60 °C for 72 h and weighed. Leaf mass per area (LMA) was calculated as the ratio between leaf dry mass and leaf area. Total nitrogen content (% dry mass, N_{green}) of leaves was determined with a CHN analyzer (Leco CHNS–932, Leco instruments, St. Joseph, MI, USA) in the Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Switzerland.

In order to determine seasonal changes in traits, we repeated the sampling and measurements in April 2007.

Leaf demography and leaf half-life

Leaf half-life (LHL) was determined demographically by following the fate of marked leaf cohorts. In April 2007, we selected one or two healthy sunlit branches per individual, marked a terminal section with 5−20 young leaves (occasionally more than 20 leaves for deciduous trees) with colored thread and counted the number of leaves between the marks. We sequentially revisited these branches in August 2007, March 2008, August 2008 and January 2009, added an additional mark at the tip of each branch and counted the living leaves in each of the marked cohorts. Side branches that started growing during the examination period were not taken into account.

For simplicity, we assumed that leaves died at a constant rate and that the number of leaves left on the original branch thus decreased exponentially (Harper, 1967). We define LHL as the time required for half of the leaves to absciss.

$$LHL = (T_2 - T_1) * \ln(1/2) / \ln(N_2/N_1) \quad \text{(eq. 1)}$$

T_1 and T_2 stand for the times at the start and the end of an interval and N_1 and N_2 for the numbers of leaves in the cohort at the start and the end of the interval, respectively. LHL was calculated based on the leaf number observed at each census. An average LHL of each cohort on each individual was the mean LHL calculated using the observed leaf number from any two out of the five censuses. Thus an average LHL was calculated from maximally ten LHLs from observational data. But usually not all of the ten LHLs can be calculated due to 100% leaf survival or deciduous event in which leaf number dropped to zero during monitoring.

Leaf-demographic analyses included 90 individuals from 32 species (8 deciduous and 24 evergreen species). Only the first cohort was included in the analysis because its data were the most complete. As it is impossible to assess the actual age of each leaf on the first cohort, we conducted the same analysis using data gathered from the following cohorts. Because we found no significant difference in the results, we reported only the result from the first cohort.

Wood density

Wood samples were collected both in September 2006 and April 2007 to determine seasonal change in wood density (WD). We used an increment borer (diameter 5.15 mm, Haglöf, Sweden) to obtain a 5 cm long core (without bark) and measured the fresh volume with a water-displacement method immediately after sampling the core in order to maintain the samples at a constant humidity. The cores were then dried at 60 °C for 72 h and weighed. Wood density was calculated as wood dry mass divided by fresh volume.

Data analysis

Univariate analyses of variance

To assess the relative importance of functional type, growth form, family, species, individual and season, we fitted classical and multilevel analyses of variance (ANOVA) for each trait and used the standard deviations of each term as a measure for the importance of each source of trait variation (Gelman, 2005, Qian & Shen, 2007). Specifically, our model for trait y_i measured on individual i ($i = 1...n$) was:

$$y_i \sim N(\mu_i, \sigma_y^2), \qquad \text{(eq. 2)}$$

with $\mu_i = \alpha_0 + \alpha_{FT(i)} + \alpha_{GF(i)} + \alpha_{season(i)} + \beta_{fam(i)} + \beta_{spec(i)} + \beta_{ind(i)}$

The mean trait value μ_i was assumed to be the sum of a grand mean a_0, the fixed effects of functional type (α_{FT}), growth form (a_{GF}) and season (α_{season}, except for LHL) and the random effects of family (β_{fam}), species (β_{spec}) and individual (β_{ind}).The random effects defined the different error levels in the multilevel analysis: $\beta_{fam} \sim N(0, \sigma_{fam}^2)$, $\beta_{spec} \sim N(0, \sigma_{spec}^2)$ and $\beta_{ind} \sim N(0, \sigma_{ind}^2)$.

The residual term corresponded to the variation among season nested within individuals (except for LHL where it corresponded to the variation among individuals). The levels of the fixed effects were evergreen vs. deciduous for functional type, tree vs. shrub for growth form and September 2006 vs. April 2007 for season. Sample size n was 397 for LMA, 90 for LHL, 333 for N_{green} and 241 for WD.

To quantify the importance of each random-effects factor for the observed

variation in a trait, we used the finite-population standard deviation of the effects as suggested by Gelman (2005). For fixed-effects factors (α_{FT}, a_{GF}, α_{season}) we computed the finite-population standard deviation as the standard deviation of the coefficients in the population of predicted values (Gelman & Hill, 2007).

We chose a Bayesian implementation of our model and used Markov chain Monte Carlo (MCMC) simulation methods in WinBUGS (Spiegelhalter, Thomas & Best, 2003, Gilks, Thomas & Spiegelhalter, 1994), run from R 2.12.2 (R Development Core Team 2011; http://www.r-project.org) via the R2WinBUGS interface (Sturtz, Ligges & Gelman, 2005), to produce a large random sample from the joint posterior distribution of its parameters. We used conventional vague priors for all parameters, i.e., $N(0,1000)$ for the grand mean a_0, $U(-3,3)$ for the regression parameters in α_{FT}, a_{GF} and α_{season}, and $U(0,10)$ for the square root of the variance components σ_y^2, σ_{tag}^2, σ_{spec}^2 and σ_{fam}^2. Bayesian posterior estimates using such vague priors numerically resemble much the estimates from maximum or restricted maximum likelihood methods (Kéry, 2010, Link & Barker, 2010), but they are exact rather than approximate, because they account for the full uncertainty in the modeled system (Gelman *et al.*, 2007). For each response, we ran three Markov chains for a sufficient length so convergence was achieved according to the "Rhat" test statistic (i.e., Rhat < 1.2). To summarize our inference from the models, we report posterior means and standard deviations (Appendix A) and plot the finite-population standard deviations of all effects as in Gelman (2005) and Qian & Shen (2007).

Bivariate analyses and analysis of covariance

To determine the general pattern of trait covariance, we first explored the overall correlation, correlations of species means and the within-species correlations, across the four functional traits in our study using Pearson correlation analysis.

In order to estimate the influence of functional type, growth form, family, species, individual and season on the relationship between pairs of trait, we decomposed the sum of products of each pair, analogous to the decomposition of sum of squares in the analysis of variance. The percent of sum of products explained by each term can be interpreted as the percent of total covariance explained by the corresponding term (Bell, 1989, He, Wang, Flynn *et al.*, 2009). The explanatory terms

in the analysis were the fixed-effects factors functional type, growth form and season and the random-effects factors family, species and individual. This analysis was implemented in GenStat software (11th edition, VSN International Ltd, UK). All of the traits were log-transformed before analysis as their distributions were strongly right-skewed.

Phylogenetic signal and evolutionary divergence analyses

To test for a phylogenetic signal in each single trait, we used Blomberg's K (Blomberg *et al.*, 2003) which is the ratio of the mean squared error of the tip data divided by the mean squared error of the data calculated using the variance-covariance matrix derived from the phylogenic tree; this observed ratio is then standardized by the ratio expected under Brownian-motion evolution (Blomberg *et al.*, 2003). A value around 1 typifies Brownian evolution characteristics and a value close to 0 indicates the lack of phylogenetic signal. We assessed the significance of the K-values by randomly shuffling traits among species 1000 times and calculating 95% confidence intervals. The phylogenic tree we used was based on the "Supertree" from Phylomatic (Webb, Ackerly & Kembel, 2008), which compiles published angiosperm phylogenies.

We also tested whether evolutionary divergences in trait-pairs showed similar correlation pattern as the cross-species analyses with phylogenetically independent contrasts (PICs) (Felsenstein, 1985). We calculated PICs for each trait using package "ape" in R (Paradis, Claude & Strimmer, 2004).

Results

Univariate analyses of variance

Overall, LMA varied 5-fold (38–156 g/cm^2), N_{green} varied 4-fold (1.0–4.3 %), LHL varied 20-fold (56–1140 days) and WD varied 2-fold (0.36–0.76 g/cm^3) among species. In comparison, LMA varied 7-fold (27–198 g/cm^2), N_{green} varied 6-fold (0.8–5.0 %), LHL varied 40-fold (56–2211 days) and WD varied 3-fold (0.25–1.2 g/cm^3) within species. Species mean values of each trait are listed in Appendix B.

LMA, N_{green} and WD showed similar patterns of effects in the multilevel

ANOVA, with functional type having the largest explanatory power, family, species and season having intermediate power, growth form and variation among individuals having the lowest explanatory power. For LHL, functional type had similar explanatory power as family, species and growth form, yet residual variation was particularly large compared with the explanatory terms, which indicated that there was large variation within species for this trait. For example in *Camellia oleifera*, LHL ranged from 256 to 2211 days among eight individuals. The classical ANOVA results (Appendix C (a)) were qualitatively very similar to multilevel ANOVA results, so only the latter are presented (Fig. 1).

For N_{green} and LMA, phylogenetic signal was significantly greater than random expectations (LMA: K=0.596, K_{rand}=0.257, 95 % CI=0.371–0.514; for N_{green}: K=0.767, K_{rand}=0.368, 95 % CI=0.245–0.515). The two other traits, WD and LHL, showed no significant phylogenetic signal (WD: K=0.4, K_{rand}=0.367, 95 % CI=0.259–0.527, LHL: K=0.445, K_{rand}=0.436, 95 % CI=0.293–0.66).

The wide range of soil nitrogen content (0.8–9.65 g/kg) and organic matter content (6–306 g/kg) at our study site was testified to the large heterogeneity of abiotic conditions within the site. Nevertheless, soil nitrogen content and organic matter content explained only a very small proportion of trait variation and no significant relationship between any of the traits and soil properties could be found (test for soil nitrogen content shown in Appendix C (b)).

Bivariate analyses and evolutionary divergence analyses

LMA, LHL and WD were significantly positively correlated with each other and significantly negatively correlated with N_{green} (Table 2). Species mean correlations were much stronger than within-species correlations. Removing the influence of common phylogenetic history by using PICs yielded almost the same results as species mean correlations (Table 2).

Analysis of covariance

When the overall covariance among traits were partitioned, functional type explained significant amounts of the total covariation between trait-pairs (except for LHL–WD; Fig. 3). Growth form was less important in most correlations (except for N_{green}–LHL, growth form explained 44 % of the total covariance). For N_{green}–LMA and

LMA–LHL, growth form had covariance components with different sign from the overall correlations. The covariance component for the taxonomic term family (except for N_{green}–LMA) was rarely significant, which was consistent with the results from the analysis of PICs demonstrating the low influence of phylogeny on trait correlations. The small but significant covariance components for species had the same signs as the overall correlations. Within species, the covariance components were all non-significant (Fig. 3), indicating that the leaf economics spectrum observed here was not a simple consequence of environmental or developmental variation among individuals within species.

Discussion

Patterns of variation in functional traits

We partitioned the variation in four functional traits: leaf half-life (LHL), leaf mass per area (LMA), nitrogen concentration in green leaves (N_{green}) and wood density (WD). The large variation of leaf and wood traits in the 45 woody species showed that many strategies co-occur in a single habitat. The contrast between deciduous and evergreen species explained the largest amount of univariate variation in three traits: evergreen species had greater LMA and WD and lower N_{green} than deciduous species. The "defining" trait for functional type, i.e. LHL, however, didn't separate evergreen species from deciduous species clearly. Some evergreen species had LHL shorter than deciduous species. For example, evergreen species *Ilex chinensis* had a LHL of 197 days, while deciduous species *Rhus chinensis* had a LHL of 259 days (Fig. 2). Many assumptions regarding deciduousness (e.g., evergreen species have smaller N_{green}, lower photosynthetic capacity and greater LMA) are applied only to the extent that evergreens have long leaf life-span. It has been hypothesized that evergreen species with relatively short-lived leaves should be more similar to deciduous species with regard to other leaf functional traits (Reich *et al.*, 1992). However, within the single forest community studied here this was not the case. There was no overlap between evergreen and deciduous species if they were plotted in the bivariate trait space of LMA–N_{green} (Fig. 4). The only slight exception to the rule was the deciduous species *Quercus variabilis* with a relatively long LHL (331 days) and a trait syndrome that approached that of evergreen species. Nonetheless, our study shows

the distinction between evergreen and deciduous species are not restricted to their leaf half-life. Rather, their physiological and morphological attributes reflected different strategies plants obtained during evolutionary processes.

Leaf trait values were strongly season-dependent: often the variance component explained by differences between seasons was as large (LMA, WD) or even larger (N_{green}) than the variance component explained by differences between species (Fig. 1). This suggests that the investigated species have a high seasonal variation, probably reflecting a shift between growth (spring) and storage (summer/autumn) functions of the trees (Chapin & Kedrowski, 1983, Chapin, Schulze & Mooney, 1990). For example, greater N_{green} in April 2007 could reflect the demand for fast acquisition of assimilates at the beginning of the growing season, whereas the lower value in September 2006 could reflect accumulation towards the end of the growing season. Our results show that it is important to consider seasonality when measuring leaf traits, and that the same leaf trait measured at different time points may reflect different aspects of the functional ecology of a species. Compared to this within-species and within-individual temporal variation in leaf traits, variation among individual within species was relatively small. This shows that working with (seasonally standardized) species means captures the relevant functional variation in leaf traits in a community (but see Baraloto, Paine, Patino *et al.*, 2010b).

Patterns of covariation in functional traits

Strong correlations among N_{green}, LMA and LHL were found both for individual data and for species means in the studied forest community (Table 2). This is consistent with results from global compilations of data across different ecosystem types and plant functional groups, including herbaceous and woody species (Wright *et al.*, 2004). The range of trait values covered in our study was remarkable compared to the global dataset: LMA, N_{green} and LHL in our study covered 7%−75%, 16%−97.5% and 2.5%−90% of trait distribution from global database (traits are all log_{10}-transformed), which shows in a single community functional traits vary widely. The slopes of regression in our study in N_{green}−LMA (-1.06, 95% CI: -0.88−-1.29) and LHL−LMA (2.54, 95% CI: 1.92−3.36) were significantly steeper than those in a global dataset (-0.78, 95% CI: -0.76−-0.81 for N_{green}−LMA and 1.71, 95% CI:

1.61−1.81 for LL−LMA; Fig. 5). This indicates that, in our forest community, N_{green} decreases and LHL increases in greater proportion with increasing LMA than in global patterns. This occurred mainly because our study only included trees and shrubs, which had generally low LMA values and high N_{green} values (Wright *et al.*, 2004). Our results suggest although there is global generality of plant functioning (Reich *et al.*, 1997), the coefficient of trait correlation between species in different biomes can vary substantially.

LMA and LHL (or more generally leaf life-span) capture one of the major axes of functional trait variation in plants (Westoby, Falster, Moles *et al.*, 2002). Long-lived, dense or thick leaves are expensive to build, but they enable plants to withstand physical and herbivore damage. The dense structure of expensive leaves reduces photosynthetic capacity by diluting the proportion of leaf tissue allocated to photosynthetic enzymes (reflected in lower leaf nitrogen concentration) and can lead to CO_2 diffusion limitation (Field & Mooney, 1986, Reich *et al.*, 1992). On the other hand, short-lived, thin leaves are cheap to build, and they have a low LMA, leading to a large light-capturing surface per unit biomass invested. But these leaves are susceptible to physical and herbivore damage. It should be noted that we used LHL, the time until half of all leaves in a cohort had died, instead of leaf life-span which is widely used but lacks consistency in definition. For example, leaf life-span may be estimated from the maximum survival time of leaves from one species, or from the median or mean survival time of leaves when maximum survival time is impossible to be estimated due to short durations of observation. This inconsistency in definition or measurement can lead to errors when comparing leaf life-span among studies. Therefore we advocate using leaf demographic measures and in particular, leaf half-life.

We also found for both individual data and for species means that WD was negatively related to N_{green}, and positively related to LHL and LMA (Table 2). This suggests that the syndrome of correlations among functional traits could be extended beyond leaf traits to this important wood trait within the studied community. WD has attracted considerable interest as it is related to growth rate, survival, mechanical strength and resistance to herbivory (Chave *et al.*, 2009). Meanwhile, similar relations have been proposed for the leaf: species with short-lived, physiologically active leaves have high growth but low survival (Poorter & Bongers, 2006). Considering these previous findings it was logical to expect a link between WD and

the leaf traits in our study. Similar correlations between leaf and wood traits have also been found in other studies. For example, a study of inter-specific correlation patterns among Panamanian dry forest trees reported that WD was negatively correlated with photosynthetic capacity (Santiago *et al.*, 2004). WD was also positively correlated to LMA and LHL in 32 co-existing species on the Bonin Islands (Ishida *et al.*, 2008). However, the large compilation of Wright *et al.* (2007) could not find a consistent overall correlation between WD and traits included in their leaf economics spectrum across 2134 woody species from seven Neotropical forests. Similarly, Baraloto *et al.* (2010a) found that in lowland Neotropical forests in French Guiana leaf and wood traits were uncorrelated.

It seems that the coordination between leaf and wood traits is stronger within communities than across sites. One explanation for this inconsistent pattern is that there are two different situations where functional trait coordination can be expected. First, different strategies are found among sites which differ in environmental conditions. Second, different strategies allow species to coexist in a single community by specializing on different sections of the environment. We argue that the second situation is perhaps more common than expected. Functional coordination between leaf and wood traits would only be observed if different strategies along a spectrum of trait correlations are favoured by the force of competitive exclusion within communities (Westoby *et al.*, 2002), but this coordination diminished when studied across communities because of the contrasting environments and different species compositions.

The significant contribution of functional type to covariance of all trait pairs showed the distinction between evergreen and deciduous species. The small but significant covariance components for species after correcting for functional type, growth form and family indicated that trait integration among species was not fully explained by the distinction between evergreen and deciduous species, trees and shrubs, and families. Thus, natural selection additionally constrains different species to position themselves along a spectrum in the trait space to obtain maximum fitness (Reich *et al.*, 1997). The small covariance components for residual variation among individuals within species (Fig. 3), which was in line with other studies on functional trait correlations between and within species (e.g., He *et al.*, 2009), indicated that trade-offs and functional trait spectrum were not caused by environmental differences experienced by individuals.

Trait coordination in an evolutionary context

In our study, two functional traits showed significant phylogenetic signal (LMA and N_{green}) at family level and two did not (WD and LHL). The high degree of phylogenetic niche conservatism of LMA and N_{green} implies that there has been little evolutionary change since the species' divergence from a common ancestor (family) or that parallel evolutionary changes have occurred independently since divergence (Ackerly, 2003). WD showed no phylogenetic signal at family level, yet there was significant inter-generic and inter-specific variation (see Appendix C (a) for significance tests), which indicates the largest evolutionary divergences in wood density could have occurred relatively recently (Chave, Muller-Landau, Baker *et al.*, 2006, Swenson & Enquist, 2007).

Despite the phylogenetic signal in LMA and N_{green} the correlation between the two traits was barely affected by phylogeny as shown by the result of PIC analysis (Table 2). Indeed, all trait-pair correlations remained strong in this analysis, indicating that they were not merely due to contrasting characteristics of major plant lineages but rather reflected patterns of correlated evolutionary change in different lineages rather than common phylogenic history. (Ackerly & Reich, 1999). For example, species with low LMA (short-lived leaves) and low N_{green} (low leaf nitrogen and presumably low maximum photosynthetic rate) should be rapidly eliminated by selection due to both low survival and slow growth (Ackerly, 2003). Conversely, a "Darwinian demon" with high LMA and high N_{green} obviously has not evolved, because if it would have it should have displaced all other strategy types due to both high survival and fast growth. Our result shows that evolutionary coordination between traits is robust independent of the phylogenetic signal contained in a single trait.

For the trade-off between the phylogenetically conserved N_{green} and WD it may be postulated that it was driven by N_{green}, whose value was first fixed deep in evolution when the divergence of family appeared. Under this hypothesis, species from families with high N_{green} evolved to have low WD and vice versa, probably because this trait-pair combination was favoured by adaptive evolution within ancient communities.

Phylogenetically independent contrasts (PICs) has been widely used in comparative analysis of functional traits (Wright *et al.*, 2007, Ackerly *et al.*, 1999, Swenson *et al.*, 2007), while the phylogenetic signal for a single trait was rarely

reported. The combination of using phylogenetic signal and PICs methods provides us the opportunity to evaluate influences of evolution on both single trait and pair of traits. Phylogenetically independent contrasts (PICs) has been widely used in comparative analysis of functional traits (Wright *et al.*, 2007, Ackerly *et al.*, 1999, Swenson *et al.*, 2007), while the phylogenetic signal for a single trait was rarely reported. The combination of using phylogenetic signal and PICs methods provides us the opportunity to evaluate influences of evolution on both single trait and pair of traits.

Conclusions

Functional trait variation and covariation among species across spatial scales has been studied intensively in the past to gain insight into plant adaptations to the environment. However, a large proportion of the inter-specific variance in traits, e.g. 36 % in SLA and 38 % in leaf nitrogen per mass, is found at the local scale within communities (Wright *et al.*, 2004). We found that despite substantial heterogeneity in time and space, functional type and species were the main sources of trait variation. When considering trait-pair correlations, we found again functional type and species to be the most important sources of covariance. Species could be placed along a spectrum—similar to the leaf economics spectrum reported from different communities—which runs from deciduous species with short-lived, thin leaves and light wood to evergreen species with long-lived, thick leaves and dense wood. The small covariation between the investigated functional traits at the within-species level showed that the functional trait coordination was not merely a result of environmental variability. With the help of phylogenetic signal and PIC analyses we could confirm that the observed functional trait spectrum reflected evolutionary coordination of leaf and wood traits within a single community and that natural selection must have played an important role in shaping the spectrum occurring within a single community.

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Table 1. Species list (n=45) with functional type, growth form and number of individuals.

Family	Genus	Species	Functional type	Growth form	Number
Anacardiaceae	*Choerospondias*	*axillaris*	deciduous	tree	5
	Pistacia	*chinensis*	deciduous	tree	16
	Rhus	*chinensis*	deciduous	tree	9
		punjabensis	deciduous	tree	1
	Toxicodendron	*succedaneum*	deciduous	tree	9
Aquifoliaceae	*Ilex*	*chinensis*	evergreen	shrub	6
		szechwanensis	evergreen	tree	10
Araliaceae	*Aralia*	*chinensis*	deciduous	shrub	5
	Kalopanax	*pictus*	deciduous	tree	6
Cornaceae	*Cornus*	*controversa*	deciduous	tree	5
Ebenaceae	*Diospyros*	*kaki*	deciduous	tree	1
Elaeocarpaceae	*Elaeocarpus*	*japonicus*	evergreen	tree	8
Euphorbiaceae	*Mallotus*	*philippinensis*	deciduous	tree	5
		tenuifolius	evergreen	tree	5
Fagaceae	*Betula*	*luminifera*	deciduous	tree	8
	Castanopsis	*carlesii*	evergreen	tree	4
		fargesii	evergreen	tree	6
		sp	evergreen	tree	4
	Cyclobalanopsis	*glauca*	evergreen	tree	14
	Lithocarpus	*harlandii*	evergreen	tree	10
	Quercus	*serrata*	deciduous	tree	12
		variabilis	deciduous	tree	11
Juglandaceae	*Platycarya*	*strobilacea*	deciduous	tree	6
	Pterocarya	*stenoptera*	deciduous	tree	4
Lauraceae	*Cinnamomm*	*bodinieri*	evergreen	tree	8
	Lindera	*communis*	evergreen	shrub	5
	Machilus	*pingii*	evergreen	tree	5
Moraceae	*Ficus*	*henryi*	evergreen	shrub	5
		heterophylla	deciduous	tree	1
Myrsinaceae	*Myrsine*	*africana*	evergreen	shrub	8
Olacaceae	*Schoepfia*	*jasminodora*	deciduous	tree	2
Pittosporaceae	*Pittosporum*	*podocarpum*	evergreen	shrub	7
		sp	evergreen	shrub	3
Rosaceae	*Photinia*	*davidsoniae*	evergreen	tree	5
	Pyracantha	*fortuneana*	evergreen	tree	5
Rutaceae	*Zanthoxylum*	*ovalifolium*	deciduous	shrub	6
Symplocaceae	*Symplocos*	*anomala*	deciduous	tree	5
		laurina	evergreen	tree	10
		paniculata	evergreen	tree	4
		stellaris	evergreen	tree	8
		sumuntia	evergreen	tree	10
Theaceae	*Camellia*	*oleifera*	evergreen	shrub	13
	Eurya	*alata*	evergreen	shrub	6
		japonica	evergreen	shrub	7
Ulmaceae	*Celtis*	*vardervoetiana*	deciduous	tree	1

Table 2. Correlations between traits: (1) Overall correlations; (2) correlations between species means; (3) inter-specific evolutionary divergence correlations using phylogenetically independent contrasts (PICs); (4) within-species correlations. Numbers show Pearson correlation coefficient. Traits were log-10 transformed prior to analysis. ***: $P < 0.001$; **: $P < 0.01$; *: $P < 0.05$.

	Overall	Species mean	PICs	Within-species
N_{green}–LMA	–0.781***	–0.779***	–0.745***	–0.615***
N_{green}–LHL	–0.308***	–0.535***	–0.435**	0.135
N_{green}–WD	–0.371***	–0.564***	–0.605***	0.000
LMA–LHL	0.348***	0.654***	0.524**	0.028
LMA–WD	0.357***	0.416**	0.460**	0.030
LHL–WD	0.279*	0.378*	0.380*	–0.139

Fig. 1. Display of standard deviations of fixed or random effects from Bayesian multilevel analyses of variance for each trait. They were estimated for both fixed and random effects (see text). Circles are estimated posterior means of effect size, short thick lines are the 50 % posterior credible intervals and long thin lines are the 95 % posterior credible intervals. N_{green}: nitrogen concentration in green leaves; LHL: leaf half-life; LMA: leaf mass per area; WD: wood density.

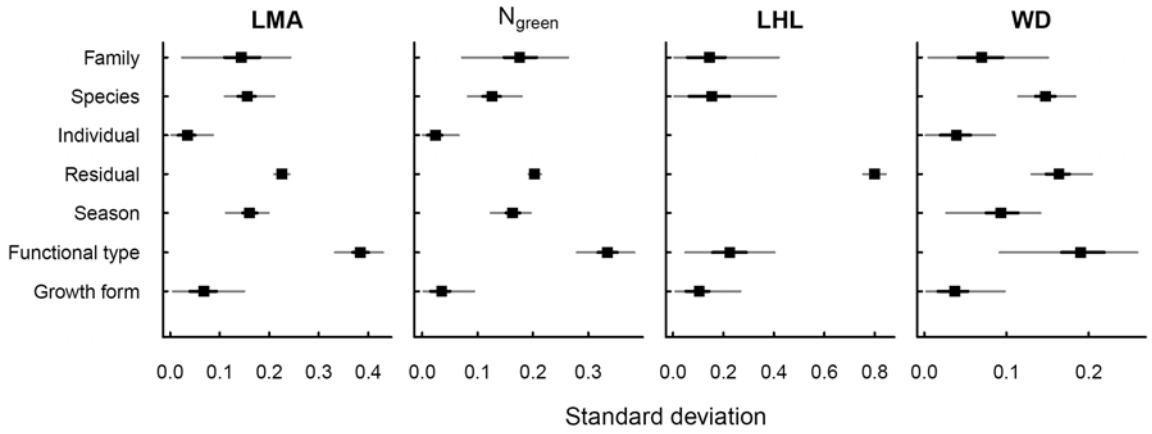


Fig. 2. Leaf half-life (LHL) of species. Points indicate species mean and lines indicate the range of data. The numbers in the brackets indicate numbers of individuals, branches and leaves used in estimating LHL. Circles represent evergreen species and solid points represent deciduous species. For species taxonomy, see Table 1.

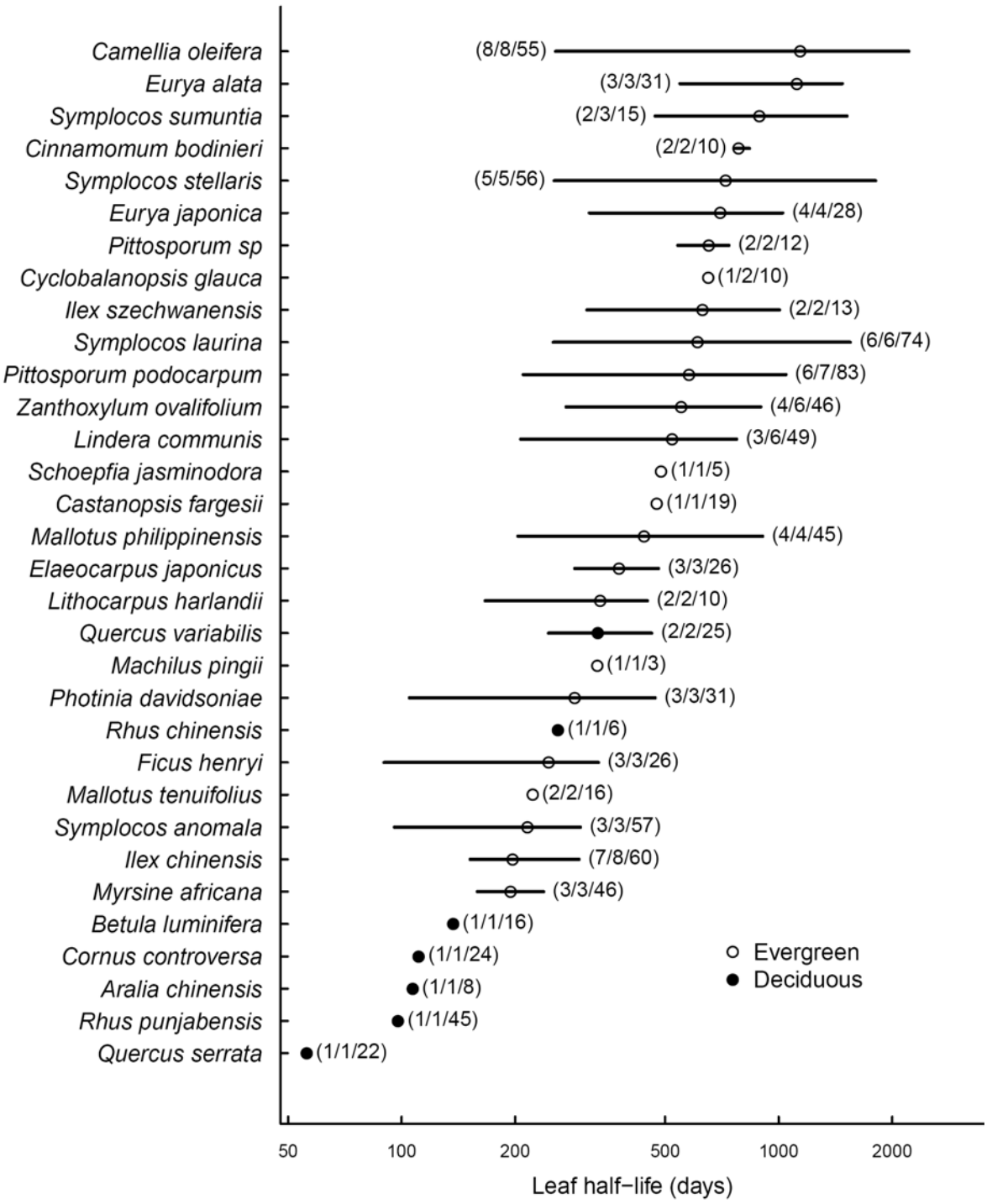


Fig. 3. Partitioning of sums of products between pairs of traits. Sections with solid filling represent fixed factors (season, functional type and growth form), while sections with hatching lines represent random factors (family, species and individual). Sections with no shadings represent sum of products explained by residual covariation. ***: P < 0.001; **: P < 0.01; *: P < 0.05; +: P<0.05 (contributions to sums of products from negative covariance components). N_{green}: nitrogen concentration in green leaves; LHL: leaf half-life; LMA: leaf mass per area; WD: wood density.

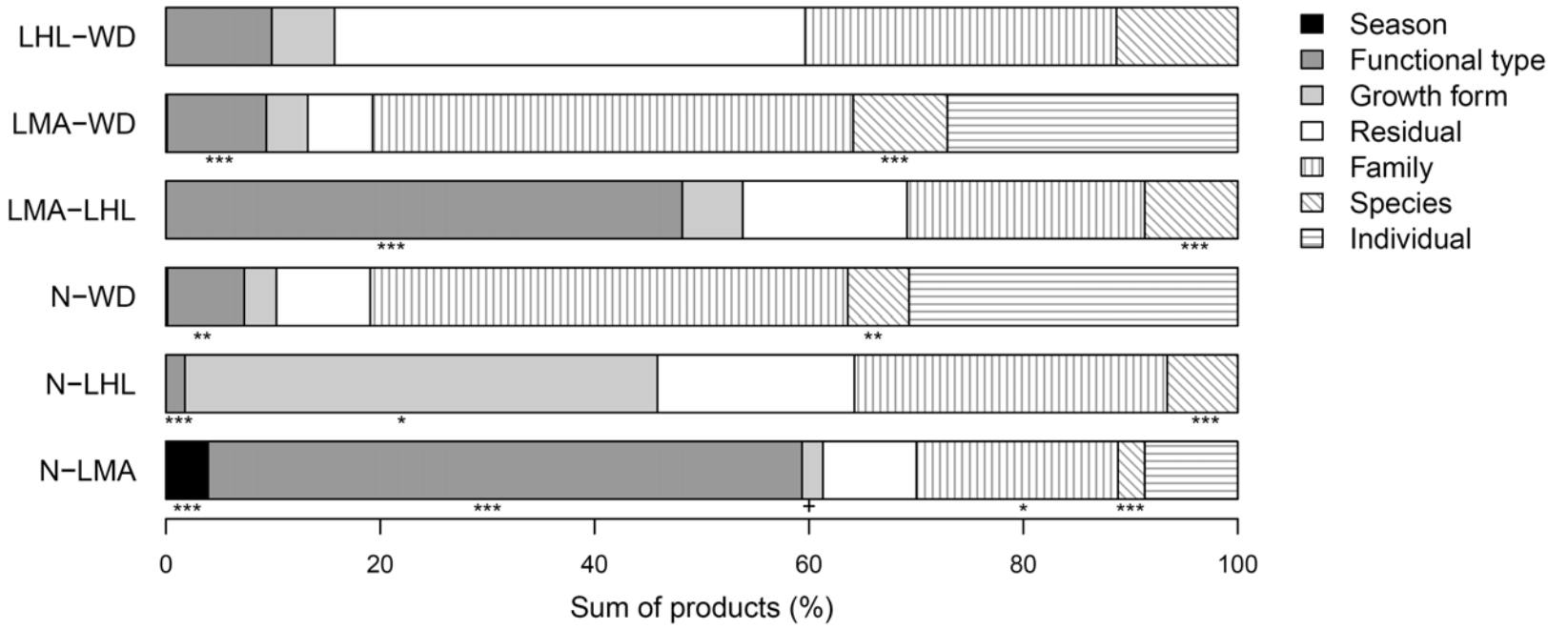


Fig. 4. Correlation between species means of N_{green} and leaf mass per area (LMA). Circles represent evergreen species and solid points represent deciduous species. The size and circles and points indicate species-mean leaf half-life.

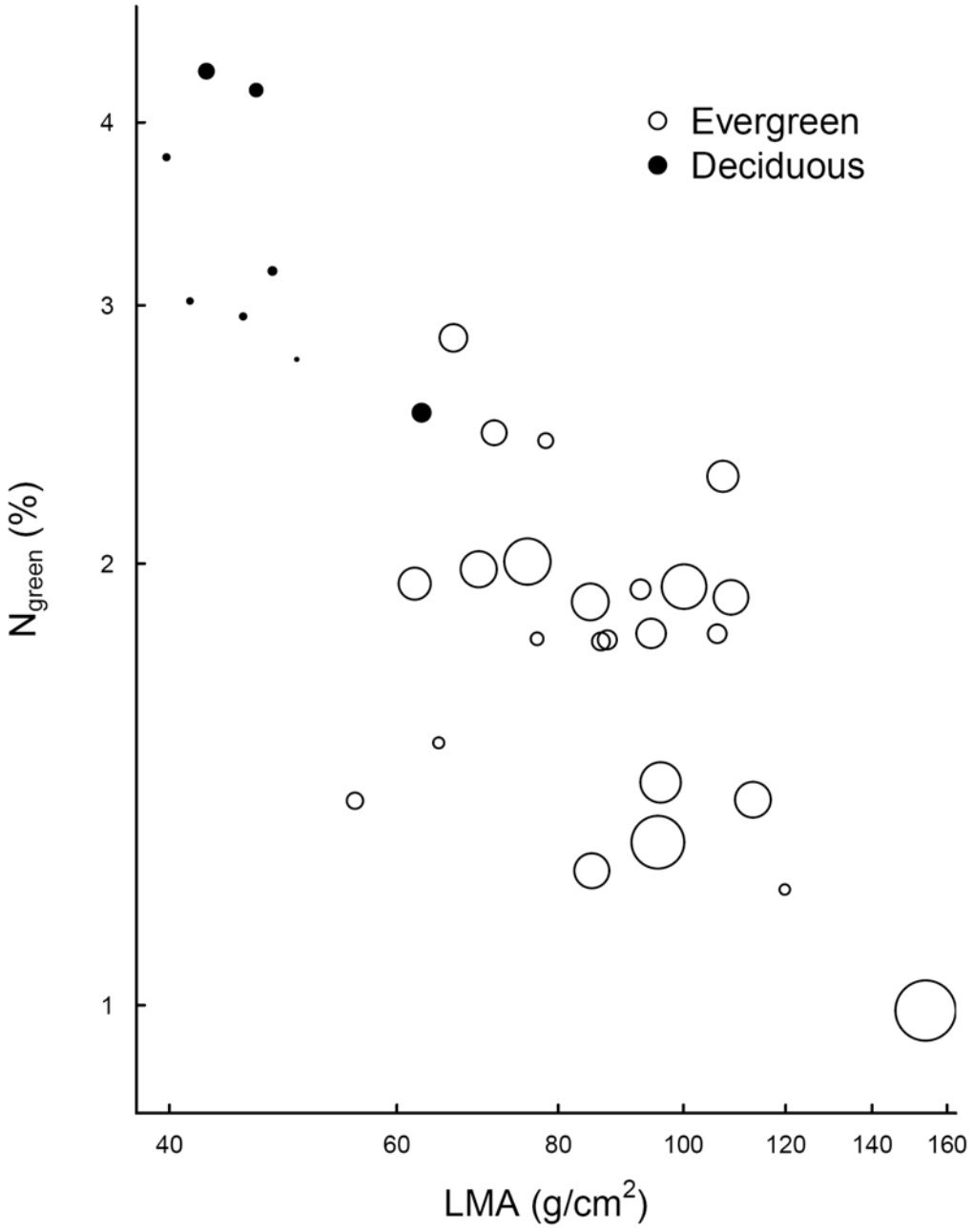
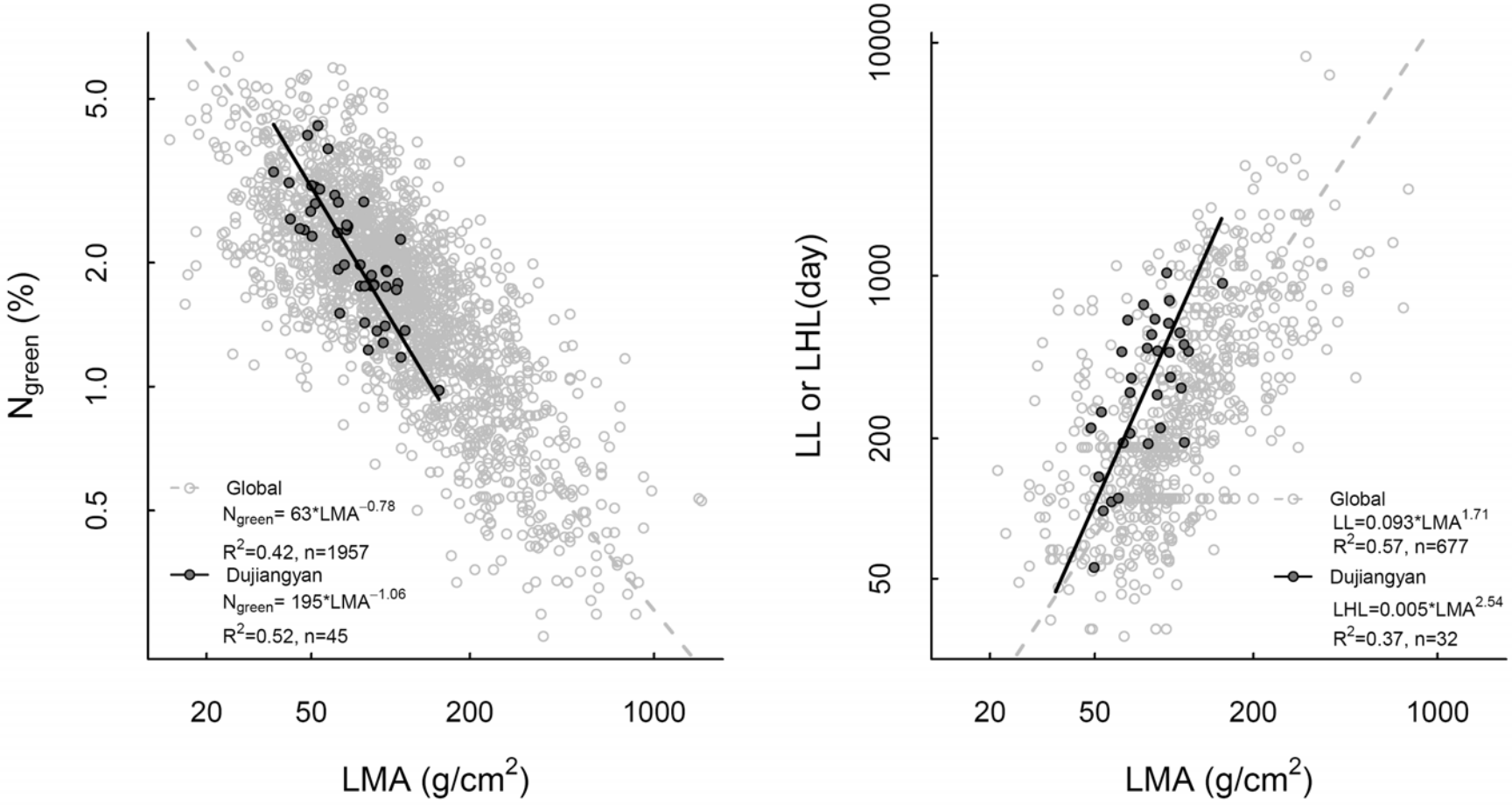


Fig. 5. Tradeoffs between leaf mass per area (LMA), nitrogen concentration in green leaves (N_{green}) and leaf half-life (LHL) for the forest community at Dujiangyan and for the global dataset from Wright *et al.* (2004). Light grey circles represent the global dataset (species-mean values), while black points represent species means from the present study.



Appendix A: Posterior means, standard deviations and credible intervals of the effect sizes from Bayesian multilevel analyses of variance for each of the four measured traits. Rhat shows how well convergence was achieved (the closer to 1 the better). N_{green}: nitrogen concentration in green leaves; LMA: leaf mass per area; LHL: leaf half-life; WD: wood density; GF: growth form; FT: functional type.

Trait	Source	Mean	SD	2.50%	25%	50%	75%	97.50%	Rhat
LMA	GF	0.068	0.038	0.006	0.040	0.066	0.093	0.149	1.001
	FT	0.384	0.024	0.333	0.368	0.385	0.401	0.430	1.001
	Season	0.160	0.022	0.113	0.147	0.162	0.175	0.199	1.003
	Residual	0.226	0.008	0.210	0.221	0.226	0.231	0.241	1.398
	Individual	0.035	0.023	0.002	0.016	0.032	0.050	0.086	1.010
	Species	0.155	0.026	0.110	0.137	0.153	0.172	0.210	1.002
	Family	0.144	0.055	0.024	0.110	0.148	0.181	0.243	1.005
N_{green}	GF	0.035	0.025	0.003	0.015	0.030	0.050	0.094	1.001
	FT	0.334	0.026	0.280	0.318	0.335	0.352	0.383	1.001
	Season	0.163	0.019	0.124	0.152	0.165	0.177	0.196	1.005
	Residual	0.203	0.006	0.192	0.199	0.203	0.207	0.215	1.222
	Individual	0.024	0.018	0.001	0.010	0.021	0.036	0.066	1.027
	Species	0.126	0.025	0.083	0.110	0.125	0.141	0.180	1.007
	Family	0.176	0.047	0.072	0.148	0.178	0.207	0.263	1.005
WD	GF	0.037	0.026	0.003	0.017	0.033	0.053	0.098	1.001
	FT	0.190	0.042	0.092	0.167	0.195	0.219	0.259	1.001
	Season	0.093	0.029	0.027	0.075	0.096	0.114	0.141	1.001
	Residual	0.164	0.019	0.131	0.148	0.164	0.177	0.204	2.442
	Individual	0.039	0.024	0.002	0.019	0.038	0.056	0.086	1.028
	Species	0.148	0.018	0.115	0.135	0.147	0.159	0.184	1.001
	Family	0.070	0.039	0.005	0.041	0.069	0.096	0.151	1.013
LHL	GF	0.104	0.069	0.010	0.052	0.092	0.143	0.267	1.002
	FT	0.225	0.093	0.049	0.157	0.228	0.291	0.403	1.004
	Residual	0.799	0.022	0.754	0.786	0.800	0.813	0.844	1.002
	Species	0.154	0.111	0.006	0.064	0.134	0.224	0.408	1.010
	Family	0.145	0.113	0.005	0.058	0.122	0.207	0.420	1.001

Appendix B: Species mean (standard deviation) of investigated traits.

Family	Genus	Species	LMA (g/m^2)	N_{green} (%)	LHL (days)	WD (g/cm^3)
Anacardiaceae	*Choerospondias*	*axillaris*	45 (23)	2.5 (0.7)		44 (3.2)
	Pistacia	*chinensis*	68 (18)	2.4 (0.4)		71.5 (13.9)
	Rhus	*chinensis*	43 (3)	4.3 (0.5)	260	44.2 (3.7)
		punjabensis	42	3	98	51.9
	Toxicodendron	*succedaneum*	45 (14)	3.2 (0.8)		49.8 (5.1)
Aquifoliaceae	*Ilex*	*chinensis*	120 (28)	1.2 (0.2)	185 (35)	62.9 (10.7)
		szechwanensis	85 (10)	1.2 (0.1)	619 (312)	
Araliaceae	*Aralia*	*chinensis*	40 (6)	3.8 (0.2)	107	44.3 (5.9)
	Kalopanax	*pictus*	59 (24)	2.9 (0.7)		46.4 (9.8)
Cornaceae	*Cornus*	*controversa*	46 (16)	2.9 (0.4)	111	42.3 (1.1)
Ebenaceae	*Diospyros*	*kaki*	40 (18)	2.6 (1.2)		67.2
Elaeocarpaceae	*Elaeocarpus*	*japonicus*	93 (13)	1.9 (0.3)	351 (87)	53.9 (12.9)
Euphorbiaceae	*Mallotus*	*philippinensis*	71 (14)	2.5 (0.2)	440 (327)	62.8 (3.1)
		tenuifolius	47 (17)	4.2 (1.2)	223	42 (12.9)
Fagaceae	*Betula*	*luminifera*	48 (14)	3.2 (0.9)	137	48.5 (4.9)
	Castanopsis	*carlesii*	80 (11)	1.8 (0.1)		68.4 (13.4)
		fargesii	87 (11)	1.8 (0.1)	335 (243)	60.5 (17.6)
		sp	89 (9)	1.8 (0.2)		62.8 (9.9)
	Cyclobalanopsis	*glauca*	85 (12)	1.9 (0.3)	650	68.4 (10.7)
	Lithocarpus	*harlandii*	86 (12)	1.8 (0.2)	314 (142)	60 (9.1)
	Quercus	*serrata*	50 (18)	2.8 (0.8)	56	69.8 (6.2)
		variabilis	63 (20)	2.5 (0.6)	317 (124)	76.7 (12.6)
Juglandaceae	*Platycarya*	*strobilacea*	52 (13)	2.9 (0.9)		52.1 (3.9)
	Pterocarya	*stenoptera*	42 (7)	3.1 (0.2)		36.2 (2.7)
Lauraceae	*Cinnamomum*	*bodinieri*	100 (14)	1.9 (0.2)	791 (39)	52.8 (3.6)
	Lindera	*communis*	94 (14)	1.8 (0.4)	522 (236)	
	Machilus	*pingii*	106 (20)	1.8 (0.2)	330	49.4 (1.9)
Moraceae	*Ficus*	*henryi*	78 (16)	2.4 (0.4)	262 (116)	48.3 (7.5)
		heterophylla	47 (18)	2.4 (1.1)		68.4
Myrsinaceae	*Myrsine*	*africana*	64 (13)	1.5 (0.1)	195 (40)	
Olacaceae	*Schoepfia*	*jasminodora*	66	2.9 (0.7)	488	71.2 (22.8)
Pittosporaceae	*Pittosporum*	*podocarpum*	62 (11)	1.9 (0.2)	567 (382)	72.1
		sp	69 (12)	2 (0.2)	639 (114)	76.7 (22.8)
Rosaceae	*Photinia*	*davidsoniae*	56	1.4 (0.2)	288 (258)	74.6
	Pyracantha	*fortuneana*	75 (12)	1.4 (0.2)		
Rutaceae	*Zanthoxylum*	*ovalifolium*	107 (20)	2.3 (0.3)	551 (238)	72.3 (4.9)
Symplocaceae	*Symplocos*	*anomala*	77 (19)	1.8 (0.3)	225 (100)	60.5 (6.3)
		laurina	113 (14)	1.4 (0.2)	634 (532)	72.7 (26.6)
		paniculata	42 (6)	2.6 (0.1)		58.8 (5.7)
		stellaris	109 (21)	1.9 (1)	613 (570)	55.8 (6.9)
		sumuntia	76 (14)	2 (0.3)	819 (604)	55.7 (3.5)
Theaceae	*Camellia*	*oleifera*	154 (25)	1 (0.2)	1069 (682)	69.2 (6.6)
	Eurya	*alata*	96 (13)	1.3 (0.2)	934 (433)	61.6 (8.9)
		japonica	96 (13)	1.4 (0.2)	715 (300)	60.1 (2.6)
Ulmaceae	*Celtis*	*vardervoetiana*	30 (8)	3.5 (1.4)		51.4 (4.7)

Appendix C: ANOVA of traits without (a) or with soil nitrogen as covariate (b). Df.: degree of freedom; %SS: percent contribution to total sum of squares; P: level of significance; LogNsoil: soil nitrogen content (log scale). For other abbreviation see Appendix A.

（a）

	LMA			N_{green}		
	Df.	%SS	P	Df.	%SS	P
Season	1	0.24	0.086	1	2.43	0.000
FT	1	38.34	0.000	1	45.52	0.000
GF	1	0.15	0.526	1	2.03	0.007
Family	19	17.22	0.029	19	20.29	0.021
Genus	13	4.14	0.590	13	4.50	0.157
Species	11	3.97	0.000	11	2.06	0.002
Individual	218	17.96	0.434	211	14.02	0.999
Residual	223	17.97		75	9.16	
Total	487	100.00		332	100.00	

	LHL			WD		
	Df.	%SS	P	Df.	%SS	P
Season				1	0.16	0.325
FT	1	14.14	0.015	1	7.49	0.002
GF	1	8.58	0.041	1	1.22	0.115
Family	15	17.85	0.262	18	27.09	0.805
Genus	7	5.10	0.788	11	25.77	0.005
Species	7	9.57	0.110	10	4.10	0.015
Individual				148	26.16	0.349
Residual	57	44.76		50	8.00	
Total	89	100.00		240	100.00	

(b)

	LMA			N_{green}		
	Df.	%SS	P	Df.	%SS	P
LogNsoil	1	0.37	0.192	1	0.54	0.108
Season	1	0.23	0.255	1	1.97	0.021
FT	1	32.81	0.000	1	40.98	0.000
GF	1	0.01	1.000	1	1.30	0.472
Family	18	27.82	0.088	17	28.75	0.075
Genus	6	3.61	0.457	7	1.29	0.922
Species	7	3.92	0.020	7	4.01	0.013
Individual	55	11.71	0.210	51	10.20	0.950
Residual	110	19.52		33	10.98	
Total		100.00			100.00	

	LHL			WD		
	Df.	%SS	P	Df.	%SS	P
LogNsoil	1	1.26	0.366	1	1.24	0.131
Season				1	0.28	0.458
FT	1	12.60	0.084	1	10.08	0.035
GF	1	15.62	0.006	1	5.20	0.321
Family	12	20.69	0.274	16	30.90	0.288
Genus	3	3.54	0.739	6	18.13	0.159
Species	5	13.65	0.146	4	4.13	0.117
Individual				38	19.79	0.447
Residual	22	32.63		21	1.24	
Total		100.00			100.00	

GENERAL DISCUSSION

The large number of species coexisting in a forest community remains an intriguing phenomenon in forest ecology. It is often assumed that the heterogeneity of resources in a common habitat provides a variety of niches for different species to specialize in, whereas others emphasize dispersal limitations, which can produce aggregated patterns through neutral mechanisms, assuming that individuals of every species have the same set of demographic rates. This thesis aims to evaluate if and how resource (light) specialization of species coexisting in forest understory is conveyed by functional traits and how season, seedling age, seedling size and functional type influence it. I emphasize the light-use strategies deployed by seedlings and the life-history strategy by adult plants. I found that growth rates were mostly conveyed by net assimilation rate in a shade-house experiment irrespective of light availability (Chapter 1) whereas seedling performance in the field was mostly determined by wood density (Chapter 3). Performance trade-offs which indicate resource specialization were observed both in the shade-house and transplanting experiments, even though temporal variability and plant age had large effects on the results (Chapters 2 and 3). I found large variation in relative growth rate, survival, and functional traits in seedling and adult plants (Chapters 1 and 4). Finally, among adult plants, the within-community leaf economic spectrum corresponded well to the reported global leaf economics spectrum, extended by the dimension of wood density (Chapter 4). The detailed discussion of all results can be found at the end of each chapter. The aim of this section is to synthesize the main results of all four chapters and to discuss them in an applied context.

Species coexistence: Niche theory or neutral process

Several theoretical models predict that certain species will dominate at a given point along an environmental gradient due to their relative competence along this gradient (Grime 1977, 1979). For example along the light gradient, I found substantial crossovers among the RGR reaction norms to light of different species, indicating that the relative competence of species varied along the light gradient (Chapter 1). I also found that species with fast growth rates in high light usually suffered from poor survival in low light (Chapter 2). In accordance with these theories, the results suggest species differ in their relative competence across a gradient of light availability.

Resource specialization leads to an important concept in community ecology, that of the ecological niche, one of the two main families of mechanisms explaining species coexistence. Although many definitions of the niche have been proposed, the definition introduced by Hutchinson (1957) is particularly widespread and useful: The niche is the set of biotic and abiotic conditions in which a species is able to persist and maintain stable population sizes. Resource partitioning, a type of niche differentiation, accounts for patterns of species richness within both animal (cf. Schoener 1974) and plant communities (cf. MacArhtur & Levins 1967), the latter of which was less recognized due to the lack of appropriate null hypotheses (Chase & Leibold 2003). In contrast to niche theory, neutral theory provides a totally different point of view regarding the mechanism of species coexistence. Niche theory assumes that individuals of every species have the same demographic rates, thus, the stochastic processes of birth, death, dispersal and speciation generate species distribution patterns (Hubbell, 1997). These opposing theories have raised constant debate in community ecology about the seemingly simple question which puzzled ecologists for decades: how do species coexist?

In my view, it may not be important to argue for niche or neutral theory. As shown in Chapters 1–3, the relative competence of species can vary with time and plant size. In the shade-house experiment (Chapters 1 and 2), seedling mortality in deep shade varied between species from 0 to 80%. Shade-tolerant species had better survival in the shade and poorer growth in the light in the first year, but all species survived well in the second year, irrespective of light availability. This shows that, after the initial phase of establishment, light availability was not the major determinant for seedling survival. In the transplant experiment (Chapter 3), neither growth nor survival in first-year seedlings was influenced by light availability, but 1.5 years after the initial transplantation, a trade-off between growth in high and low light developed.

In a real forest understory, different species have seedling banks with complex age- and size-structure. Although the range of functional traits exhibited by seedlings is shaped through evolution, each of the seedlings seeks to survive and grow according to developmental stage, multiple stresses from herbivores and pathogens, competition from other seedlings and adult plants, nutrient patches, dynamic light conditions, etc. For example, if a light-demanding species happens to germinate in the shade, it may initially grow as well as a shade-tolerant seedling waiting for a tree-fall

gap to form. A fast-growing, shade-intolerant species can thrive if a gap forms shortly after seedling establishment, whereas a shade-tolerant species will win in the end if gap formation doesn't occur until long after seedling establishment. Thus the variation in growth and survival rate in shade together with the stochastic processes of gap formation can determine species distribution in the community. Which type of plant reaches dominance is related to forest dynamics, even though species may have preferred niches to thrive.

Actually, the neutral theory is already embedded in the way niches are defined and formulated. If there are niches, there are virtually unlimited niches in all dimensions, e.g. the habitat niche, the life-form niche, the phenological niche and the regeneration niche, etc. (Grubb 1977). All of these dimensions influence plant regeneration. This was just the starting point of neutral theory, which emphasizes random processes as governing community assembly. Recently, a growing number of scientists proposed the idea that neutral and niche theory may not be mutually exclusive. Rather, they are the two ends of a spectrum of coexistence mechanism (Gravel 2006).

Strategies between and within species

Results from this thesis consistently showed that there are ecological syndromes of coexisting species with different strategies, for example between light-demanding and shade-tolerating seedlings (Chapters 1–3), or between fast-growing and nutrient-conserving adult plants (Chapter 4). These syndromes can be interpreted as opportunistic and conservative strategies. The opportunistic strategy, analogous to the r-strategy in life-history theory (Pianka, 1970), is represented by a suite of functional traits optimized to achieve fast growth over the short term. Conversely, conservative species (K-strategy) do not grow fast, rather, they invest more energy to defend themselves against herbivore and pathogen damage. Thus, in the long term they can maintain positive carbon balance in low-resource environment (Kitajima, 1994). These alternatives are the extreme ends on a gradient of strategic syndromes and most species are placed in between. Thus in a forest community with diverse coexisting species, such as the community I studied, species strategies frequently overlap, as well as functional traits which ultimately convey those strategies. One of the parameters in the growth model presented in Chapter 1, L_{min}, was the whole-plant

light compensation point and was a measure of shade tolerance. In accordance with their superior performance in high light, *Pyracantha fortuneana* and *Castanea henryi* had the highest L_{min} among each leaf habit group, whereas for most species, L_{min} was rather similar and could not be distinguished by 95% Bayesian credible intervals of the posterior distribution (Chapters 1 and 2). The small differences among species in shade tolerance may explain the failure in detecting RGR rank reversals in our study. It also shows that it is necessary to study large numbers of species to identify ecological strategy deployed by species.

In general, variation in functional traits among species was larger than within species, reflecting that genetic selection was stronger than developmental and environmental plasticity (Chapter 4). However, there was also substantial variation in functional traits within species (Chapters 1–4). One of the sources of within-species variation was temporal variability (Chapter 3). Beckage *et al.* (2005) found that variability in seedling survivorship was seven times greater across time than space, which shows that temporal variability has greater effect than e.g. the occurrence of forest gaps. Other forest types also exhibit temporal variation in seedling communities (e.g. Houle, 1994). Another source of within-species variation is environmental heterogeneity. Although natural selection prevents the occurrence of "super hero" species, individual plants are able to maximize their performance under a certain environment through plasticity. For example, for all individuals within each species, the deleterious effect of shade was compensated by enhanced SLA, and an increase in NAR was induced by increasing light availability due to a higher rate of photosynthesis per unit leaf area (Chapter 1). These results were consistent with previous studies (Givnish, 1988, Konings, 1989). Another example provided the seedlings in the transplanting experiment. Although among species there was a performance trade-off between high growth rate and low survival, seedlings exhibited both high growth rate and high survival in more than half of the species (Chapter 3). The good-in-all or poor-in-all phenomenon reflected local environmental differences: when the local environment was good, seedlings performed well and vice versa. These results, in accordance with previous studies (Seiwa, 2007), suggest that genetic differences allow species with different strategies to coexist in a heterogeneous habitat, whereas phenotypic plasticity allows individual plants to fully utilize resource patches within it.

Functional groups

Studying the ecology of every species in a diverse community is an overwhelming challenge. One approach for reducing the challenge is to categorize species into functional groups. One of the most popular criteria for categorizing species is their leaf habit, i.e. winter-deciduous and evergreen species, as used in dynamic vegetation global models (Turnbull, Paul-Victor, Schmid *et al.*, 2008). In general, plants with different leaf habits have differing functional traits (Cornelissen, Diez & Hunt, 1996, Ruiz-Robleto & Villar, 2005). However in some studies, plant functional type classification based on leaf habit alone had little utility (Powers & Tiffin, 2010). In addition, many assumptions regarding deciduousness (e.g., evergreen species have smaller N_{green}, lower photosynthetic capacity and greater LMA) apply only to the extent that evergreens also have long leaf life-span (Reich, Walters & Ellsworth, 1992).

In the current studies, leaf habit appeared to be an important aspect because seedlings and adult plants of evergreen species consistently had thicker leaves, low foliar nitrogen concentrations and low photosynthetic capacity compared to deciduous species (Chapters 1–4). Furthermore, the distinction between evergreen and deciduous species were not restricted to their leaf lifespan: evergreen species with short leaf lifespans still had low leaf nitrogen and low specific leaf area, like other evergreen species (Chapter 4). Thus I suggest that the different physiological and morphological attributes between evergreen and deciduous species reflected different strategies plants obtained during evolutionary processes. Nonetheless, there are also exceptions. In Chapter 1, *Pyracantha fortuneana*, a light-demanding evergreen species, exhibited gas-exchange characteristics similar to those of deciduous species (high photosynthetic capacity, high PNUE) as well as a fast response to increasing light availability. But the morphological and chemical characteristics of this species were similar to other evergreen species (low SLA and low leaf nitrogen). Results indicated that growth and related traits may differ among functional groups in significant ways, but in a complex pattern that does not allow simple generalizations about relative plant performance or response to resource supply rates. It is necessary to evaluate functional traits within and among clades, as many traits are constrained by evolutionary history.

Developmental stages and environment

Comparing the common species used in the shade-house experiment (Chapters 1 and 2), the transplanting experiment (Chapter 3) and the adult forest (Chapter 4), it appears the same species exhibit different functional traits between growing conditions and developmental phases. For example, seedlings tend to have greater SLA (which means thinner leaves) when growing in the shade house than in the forest understory. This phenomenon can be explained as an adaptation to the severe herbivore damage experienced in the natural habitat (Augspurger, 1984a, Augspurger, 1984b). It is also in accordance with the great importance of wood density for seedlings grown in forest understory (Chapter 3), suggesting that functional traits that can enhance leaf- or whole-plant resistance to damage are preferred in the natural habitat. The comparisons between adult trees and seedlings are more complicated. Seedlings had a wider range of SLAs than adult plants. This shows that seedlings are more flexible than adults because of the varying situations they may face. When avoidance of stress through phenotypic plasticity is not a viable strategy, seedlings are selected to tolerate stressful conditions.

The strategy taken by species can be very different from seedlings to adult trees. For example, the seedling of *Phoebe zhennan* is small, late successional and shade-tolerant, its growth remaining low even under 100% of light (Chapter 1). However, once a certain size is reached, *P. zhennan* can grow fast and reach the forest canopy. This is the case in many late-successional forest trees, whose seedlings persist in deep shade for a long time with slow growth, but where adults are usually found in high or intermediate light.

Implication for forest management

As a result of the expansion of agricultural land, logging activities and urban development, the area of forest has been reduced at unprecedented rates in recent times (Chazdon, 2003). Thus, it is the duty of forest ecologists to provide practical advice for the restoration of degraded forest and forest management.

The capacity of forest to regenerate after disturbance may mainly depend on the bevahiour of trees during the seedling stage of the life cycle. An understanding of performance trade-offs in seedlings is of particular importance for forest management.

If the performance along a resource gradient (for the seedling stage especially light) is strong, we would expect only a few species to have successful recruitment with the changed resource supply after disturbance. In contrast, if the original performance gradient is shallow, a fast recovery of ecosystem function with high species diversity may be expected.

For these subtropical woody species studied here, I found that although species exhibit light specialization (Chapter 1), there was a strong seedling performance trade-off in the shade-house experiment only in the first year (Chapter 2), which indicates that seedling size may be an important factor determining seedling performance. In the real forest understory, light availability was not the most important factor determining seedling performance (Chapter 3). Rather, seasonal competition and characteristics to resist physical or herbivory damage were more important.

Results from my experiments show that in the studied subtropical forest, performance trade-offs are variable according to seasonal variation, seedling age and size, which provides possibilities of successful restoration after disturbance once these factors are taken into account.

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SUMMARY

A major unsolved question in forest ecology is whether resource specialization can explain the coexistence of species in forest communities. Light is the major limiting resource for small seedlings growing in forest understory. Light heterogeneity is expected to lead to selection on traits that maximize plant performance under a certain light condition, resulting in a performance trade-off among species along a light-availability gradient. Although light-use strategies among coexisting species have been studied in diverse forest types before, the small number of species considered, the short duration of studies and the lack of proper methods for quantifying plant performance have limited the generality of results. Here I studied the light-use strategies in coexisting woody species from a subtropical forest in southwest China using a shade-house experiment, a transplanting experiment and mechanistic growth modeling. Furthermore, I explored the life-history strategy deployed by adult plants in this forest.

In **Chapter 1**, I study light-induced growth responses in a two-year shade-house experiment with seedlings from 14 species. I examine the responses of plant physiology, leaf morphology and biomass partitioning, as well as species-specific size-standardized relative growth rates (SGR) across a manipulated light gradient using a mechanistic model. Species exhibited various light-use strategies from those with suppressed growth in low light and high growth rate in high light, to those with low rates of light capture in high light but the ability to maintain positive net carbon gain in low light. I found that regardless of light availability, variation in a physiological trait (net assimilation rate) determined the largest amoung of variation in SGR, and that a morphological trait (specific leaf area) also substantially influenced SGR when the size-standardized analysis was employed, whereas interspecific variation in biomass allocation had little effect on plant growth.

In **Chapter 2**, I continue to explore light-use strategies of seedlings grown in the shade houses in the context of a potential performance trade-off among species along the light gradient. I found a trade-off between high-light growth rate and low-light survival; the strength of this trade-off decreased with seedling age. I detected neither significant rank retentions nor rank reversals of SGR between high and low light, but there were substantial crossovers among the SGR responses to light in different

species, indicating that at least for certain species the relative performance varied along the light gradient.

In **Chapter 3**, I study the strategies of seedlings grown in forest understory. In contrast to the shade-house experiment, light availability was not the single critical factor determining seedling performance. Seasonal competition and wood density appeared to be of even greater importance at least during the initial establishment phase. However, this study did suggest that after an initial phase, light-demanding and shade-tolerant strategies were deployed by different species and that this niche differentiation increased species coexistence in a heterogeneous habitat where the light-demanding species grew relatively faster in brighter patches and the shade-tolerant species grew faster in patches with lower light.

In **Chapter 4**, I study the variance and covariance of functional traits in adult trees in an ecological and evolutionary context. I show that variations in functional traits reflect integrated strategies of species, which can be placed along a continuous trait spectrum running from deciduous species with short-lived, thin, high-nitrogen leaves and light wood to evergreen species with long-lived, thick, low-nitrogen leaves and dense wood. This within-community spectrum corresponds well to the reported global leaf economics spectrum, extended by the dimension of wood density. Trait coordination within species was weak, indicating that the observed trait spectrum was not accentuated by environmental variation among individuals.

I conclude that the ecological spectrum running from opportunistic to conservative strategies of the different species promotes their coexistence both at the seedling and the adult stage within a community. The resulting performance trade-off reflects light-use specialization of species. However, this trade-off is influenced by ontogeny, seasonality and the various stresses that plants encounter. Although the strategy deployed by each species is modified through evolution, plant performance is not merely a reflection of the availability of resources. Rather, plant physiology ultimately determines growth through complex processes. With this dissertation, I aim to increase our understanding of mechanisms involved in plant growth, stress tolerance and inherent trade-offs.

ZUSAMMENFASSUNG

Die wichtige waldökologische Frage, in welchem Umfang Ressourcenspezialisierung die Koexistenz von Arten einer Waldgemeinschaft erklären kann, ist bis jetzt unbeantwortet. Licht ist die wichtigste limitierende Ressource für kleine Keimlinge in der untersten Vegetationsschicht des Waldes. Es wird erwartet, dass Heterogenität im Lichtangebot zur Selektion von Eigenschaften führt, die die Leistung von Pflanzen unter bestimmten Lichtbedingungen maximieren, was zu einem Leistungsausgleich (performance trade-off) zwischen Arten entlang eines Lichtgradienten führen könnte. Lichtnutzungsstrategien gemeinsam vorkommender Arten in artenreichen Waldtypen wurden schon früher untersucht, allerdings beeinträchtigte die begrenzte Anzahl der Arten, die untersucht wurden, sowie die kurze Dauer der Studien und der Mangel an geeigneten Methoden zur Quantifizierung der Pflanzenleistung die Allgemeingültigkeit dieser Ergebnisse. In meiner Arbeit untersuchte ich Lichtnutzungsstrategien gemeinsam vorkommender verholzter Arten eines subtropischen Waldes in Südwestchina mit Hilfe eines Schattenhausexperiments, eines Verpflanzungsexperiments und mechanistischer Wachstumsmodellierung. Desweiteren untersuchte ich die life-history Strategien adulter Pflanzen in diesem Wald.

In **Kapitel 1** untersuchte ich lichtinduzierte Wachstumsreaktionen in einem zwejährigen Schattenhausexperiment mit Keimlingen von 14 Arten. Ich betrachtete deren Reaktionen entlang eines Lichtgradienten im Hinblick auf Pflanzenphysiologie, Blattmorphologie, Biomasseverteilung sowie die artspezifische grössenstandardisierte relative Wachstumsrate (species-specific size-standardized relative growth rate = SGR) mit Hilfe eines mechanistischen Modells. Diese Arten zeigten verschiedene Lichtnutzungsstrategien, von unterdrücktem Wachstum unter schlechten Lichtbedingungen und einer hohen Wachstumsrate unter guten Lichtbedingungen, bis zu Strategien mit geringem Lichtnutzungspotential unter guten Lichtbedingungen, aber der Fähigkeit, einen positiven Nettokohlenstoffgewinn unter niedrigen Lichtbedingungen zu aufrechtzuerhalten. Ich fand heraus, dass unabhängig vom Lichtangebot, vor allem die Schwankungen in einer physiologischen Eigenschaft (nämlich der Nettoassimilationsrate) die SGR bestimmte, und dass auch eine morphologische Eigenschaft (die spezifische Blattfläche) die SGR wesentlich beeinflusste, wenn die grössenstandardisierte Analyse benutzt wurde, während Biomasseverteilungsmuster keinen Einfluss auf das Pflanzenwachstum hatten.

In **Kapitel 2** untersuchte ich erneut Lichtnutzungsstrategien von im Schattenhaus angezogenen Keimlingen im Hinblick auf einen potentiellen Leistungsausgleich zwischen Arten entlang eines Lichtgradienten. Ich fand einen Ausgleich zwischen der Wachstumsrate unter guten Lichtbedingungen und dem Überleben unter niedrigen Lichtbedingungen; dieser Ausgleich nahm mit zunehmendem Keimlingsalter ab. Ich fand dagegen keine signifikante Beibehaltung oder Umkehr von SGR-Rängen zwischen hohem und niedrigem Licht. Allerdings existierten beachtliche Überschneidungen zwischen SGR-Reaktionen auf Licht bei verschiedenen Arten. Dieses Ergebnis zeigt, dass, zumindest für gewisse Arten, die relative Leistung entlang des Lichtgradienten variiert.

In **Kapitel 3** untersuchte ich Strategien von Keimlingen in der unteren Bestandesschicht des Waldes. Im Gegensatz zu den Ergebnissen des Schattenhausexperiments war das Lichtangebot hier nicht der bestimmende Faktor für die Leistung der Keimlinge. Saisonale Konkurrenz und Holzdichte schienen noch wichtiger zu sein, zumindest während der Etablierungsphase. Allerdings lässt meine Arbeit vermuten, dass nach einer Anfangsphase, lichtfordernde und schattentolerante Strategien von verschiedenen Arten benutzt wurden, und dass diese Nischendifferenzierung die Artenkoexistenz in einem heterogenen Habitat förderte, wo lichtliebende Arten an Stellen mit besseren Lichtbedingungen relativ schneller wachsen, schattentolerante dagegen an Stellen mit weniger Licht.

In **Kapitel 4** untersuchte ich die Varianz und Kovarianz funktioneller Eigenschaften im Adultstadium der Baumentwicklung in einem ökologischen und einem evolutionären Zusammenhang. Die Ergebnisse zeigten, dass in einer Gemeinschaft aus verholzten Pflanzen die Schwankungen funktioneller Eigenschaften integrierte Strategien von Arten reflektieren, welche in ein kontinuierliches Spektrum eingeordnet werden können: von sommergrünen Arten mit kurzlebigen, dünnen, stickstoffreichen Blättern und leichtem Holz bis zu immergrünen Arten mit langlebigen, dicken, stickstoffarmen Blättern und dichtem Holz. Dieses Spektrum innerhalb der Gemeinschaft entspricht dem in der Literatur bereits beschriebenen globalen Blattökonomiespektrum, erweitert durch die Dimension "Holzdichte". Die Koordination von Eigenschaften innerhalb der Arten war schwach ausgeprägt. Dies

zeigt, dass das beobachtete Eigenschaftsspektrum nicht durch umwelt- und entwicklungsbedingte Schwankungen zwischen Individuen verstärkt wurde.

Ich schliesse aus meinen Ergebnissen, dass das ökologische Spektrum der verschiedenen Arten von opportunistischen bis zu konservativen Strategien ihre Koexistenz fördert, sowohl im Keimlings- als auch im Adultstadium innerhalb einer Gemeinschaft. Der sich daraus ergebende Leistungsausgleich reflektiert Ressourcen-(Licht-)nutzungsspezialisierungen der Arten. Allerdings ist dieser Ausgleich beeinflusst von Entwicklungsstadien der Pflanze, Säsonalitat und mehreren Stressfaktoren, welchen eine Pflanze ausgesetzt ist. Obwohl die Strategie einer Pflanze durch die Evolution vorgegeben ist, ist die Pflanzenleistung nicht eine blosse Reflektion des Ressourcenangebots. Im Gegenteil, die Pflanzenphysiologie bestimmt im Endeffekt das Wachstum über komplexe Vorgänge. Somit gibt es einen dringenden Bedarf, unser Verständnis der Mechanismen, die an Pflanzenwachstum, Stresstoleranz und vorgegebenen Ausgleichen beteiligt sind, auszuweiten.

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